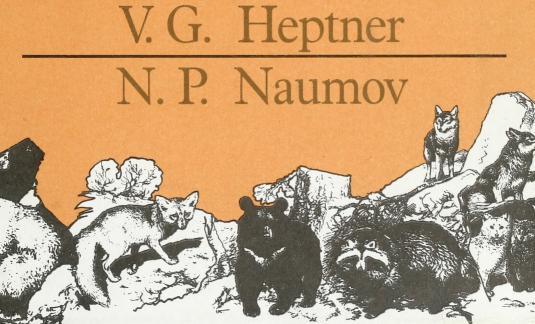
Mammals of the Soviet Union

VOLUME II
Part 1b



The present book, of the series Mammals of the Soviet Union: Sirenia and Carnivora, is the fourth volume to be published in English. Previously Volume I — Artiodactyla and Perissodactyla, Volume II, Part 2 — Carnivora (Hyenas and Cats) and Volume II, Part 3 — Pinnipeds and Toothed Whales were published in 1988, 1992, and 1996 respectively. Sea Cows, Wolves and Bears constituted the second in the series to appear.

The original Russian book is so large (982 pp.) that its publication in the English translation format would have resulted in a book of 1600 pages, which was considered too unwieldy. Therefore, it was decided to publish Volume II, Part1 — Sirenia and Carnivora, in two roughly equal parts. The first (Part 1a) consisted of the Steller's sea cow, the now-extinct marine mammal once found only around the Commander Islands in the western Bering Sea, and the Russian species of the wolf and bear families. This second half (Part 1b) comprises the various members of the weasel family, plus the introduced American raccoon.

As indicated in the foreword to the English edition of the Volume I, the senior author and editor of the series, Dr. Vladimir Georgievich Heptner, died in 1975, and did not complete the projected series. However, work continues, and Russian volumes on baleen whales, lagomorphs and dipodid rodents are now published.

A final point: since the appearance of Volume II, Part 2, the Soviet Union has disappeared. However, the series was written in the context of the former "union of republics," and it would be confusing to reedit the text to conform to the current political reality.





Mammals of the Soviet Union

Volume II Part 1b

MAMMALS OF THE SOVIET UNION

In Three Volumes

Edited by

V.G. Heptner and N.P. Naumov

Vysshaya Shkola Publishers Moscow, 1967

Mammals of the Soviet Union

Volume II, Part 1b

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Table of Contents Vol. II, Part 1b

F	amily Mustelidae (Martens, Weasels, etc.)	735
	Key for Identification of Genera in the	
	Family Mustelidae	746
	Subfamily Mustelinae	749
	Genus Martes Pinel, 1792 (Martens)	749
	Key for Identification of Species in the	
	Genus Martes	755
	Martes (Martes) zibellina (Linnaeus, 1758)	
	(Sable)	757
	Diagnosis	759
	Description	759
	Systematic Position	770
	Geographic Distribution	770
	Geographic Variation	787
	Biology	797
	Practical Significance	823
	Martes (Martes) martes (Linnaeus, 1758)	
	(Forest Marten)	825
	Diagnosis	826
	Description	826
	Systematic Position	836
	Geographic Distribution	836
	Geographic Variation	847
	Biology	850
	Practical Significance	872
	Martes (Martes) foina Erxleben, 1777	
	(Stone Marten)	874
	Diagnosis	875
	Description	876
	Systematic Position	882

Geographic Distribution	883
Geographic Variation	891
Biology	895
Practical Significance	904
Martes (Charronia) flavigula Boddaert, 1785	
(Kharza, or Yellow-throated Marten)	905
Diagnosis	905
Description	905
Systematic Position	910
Geographic Distribution	910
Geographic Variation	912
Biology	914
Practical Significance	919
Genus Gulo Storr, 1780	920
Gulo gulo (Linnaeus, 1758) (Wolverine)	925
Diagnosis	926
Description	926
Systematic Position	931
Geographic Distribution	932
Geographic Variation	940
Biology	943
Practical Significance	953
Genus Mustela (Linnaeus, 1758)	954
Key for Identification of Species in the Genus	
Mustela	962
Mustela (Mustela) nivalis Linnaeus, 1766	
(Weasel)	965
Diagnosis	966
Description	967
Systematic Position	972
Geographic Distribution	972
Geographic Variation	975
Biology	985
Practical Significance	995
Mustela (Mustela) erminea Linnaeus, 1758	
(Ermine)	995
Diagnosis	997
Description	997
Systematic Position	1003
Geographic Distribution	1003

Geographic Variation	1008
Biology	1016
Practical Significance	1029
Mustela (Mustela) altaica Pallas, 1811	
(Solongoi)	1030
Diagnosis	1031
Description	1031
Systematic Position	1036
Geographic Distribution	1037
Geographic Variation	1043
Biology	1047
Practical Significance	1051
Mustela (Mustela) sibirica Pallas, 1773	
(Kolonok or Siberian Weasel)	1051
Diagnosis	1052
Description	1052
Systematic Position	1058
Geographic Distribution	1058
Geographic Variation	1065
Biology	1069
Practical Significance	1078
Mustela (Mustela) lutreola (Linnaeus, 1761)	
(Russian, or European Mink)	1078
Diagnosis	1080
Description	1080
Systematic Position	1086
Geographic Distribution	1088
Geographic Variation	1094
Biology	1099
Practical Significance	1106
Mustela (Putorius) putorius (Linnaeus, 1758)	
(Forest, or Black, Polecat)	1107
Diagnosis	1108
Description	1108
Systematic Position	1115
Geographic Distribution	1117
Geographic Variation	1124
Biology	1126
Practical Significance	1132

Mustela (Putorius) eversmanni Lesson, 1827	
(Steppe, or White, Polecat)	1133
Diagnosis	1134
Description	1135
Systematic Position	1142
Geographic Distribution	1145
Geographic Variation	1158
Biology	1165
Practical Significance	1175
Genus Vormela Blasius, 1884	1176
Vormela peregusna (Güldenstaedt, 1770)	
(Marbled Polecat, Perevyazka)	1180
Diagnosis	1181
Description	1181
Systematic Position	1188
Geographic Distribution	1188
Geographic Variation	1194
Biology	1202
Practical Significance	1206
Genus Mellivora Storr, 1780	1207
Mellivora capensis (Schreber, 1776)	
(Ratel, or Honey Badger)	1211
Diagnosis	1211
Description	1211
Systematic Position	1217
Geographic Distribution	1217
Geographic Variation	1222
Biology	1223
Practical Significance	1228
Subfamily Melinae	1228
Genus Meles Brisson, 1762 [=Boddaert, 1785]	1228
Meles meles (Linnaeus, 1758)	
([Eurasian] Badger)	1232
Diagnosis	1234
Description	1234
Systematic Position	1242
Geographic Distribution	1242
Geographic Variation	1249
Biology	1262
Practical Significance	1281

Subfamily Lutrinae	1283
Genus Lutra Brisson, 1762 [=Brünnich, 1771]	1283
Lutra lutra* (Linnaeus, 1758) ([Eurasian] Otter)	1288
Diagnosis	1289
Description	1289
Geographic Distribution	1297
Geographic Variation	1305
Biology	1310
Practical Significance	1327
Genus Enhydra Flemming, 1822	1330
Enhydra lutris (Linnaeus, 1758) (Sea Otter,	1333
or Kalan)	
Diagnosis	1333
Description	1334
Systematic Position	1343
Geographic Distribution	1343
Geographic Variation	1348
Biology	1350
Practical Significance	1365
Supplement to the Order of Carnivores	1366
Family Procyonidae (Raccoons, etc.)	1366
Subfamily Procyoninae Gill, 1872	1373
Genus Procyon Storr, 1780	1373
Procyon (Procyon) lotor (Linnaeus, 1758)	
(American Raccoon)	1374
Diagnosis	1374
Description	1374
Systematic Position	1377
Geographic Distribution	1377
Geographic Variation	1383
Biology	1383
Practical Significance	1390
Family Mustelidae	
Mustela (Mustela) vision Schreber, 1777	
(American Mink)	1391
Diagnosis	1391
Description	1392
Systematic Position	1397

^{*}In Russian original, Lutra (Lutra)—Sci. Ed.

Geographic Distribution	1399
Geographic Variation	1403
Biology	1405
Practical Significance	1415
LITERATURE CITED	1416
INDEX OF LATIN NAMES OF TAXA*	1539

^{*}The Russian original also included an Index of Russian Names, omitted here.

Familia MUSTELIDAE Swainson, 1835

These are specialized, and in part highly specialized predators of small and very small dimensions, but with several being of moderate dimensions (the smallest species in the order belong to this family). The hind limbs are short, the trunk is strongly elongated and thin, but rarely comparatively short and compact.

The limbs are digitigrade or semi-plantigrade, but several are plantigrade with five digits on the fore- and hind-limbs. The ventral surface of the hind foot and forepaw are covered with hairs (as is, usually, the skin of the interdigital membranes) or with naked foot-pads or entirely bare; the claws are of moderate length to very large.

492 In several (individual species in the otter subfamily), bare swimming membranes between the digits are well-developed, the claws are greatly reduced (*Aonyx*), or the digits on the forelimb are shortened and closely united with one another; while on the hind limbs they are elongated and transformed into a hair-covered flipper (*Enhydra*). The claws are not retractile and the phalanges of the digits have a normal articulating surface (the last phalanges cannot bend far upwards). The vertebral column is extremely flexible—more movable than in representatives of the preceding families [Canidae, Ursidae; see vol. II, pt. 1a].

The skull is relatively small, with shortened facial parts and broadened, usually swollen braincase. In the majority, the facial portion is strongly shortened and the disproportion of the skull is noticeable; in some, it is more proportional, but the facial portion is always shorter than the braincase. In small forms, the tubercles, crests, etc. of the skull are usually weakly developed, and in large forms, they are very well-defined. The line of the upper profile is usually straight, without noticeable frontal elevation and the skull is low, as if flattened. In several, the skull is quite high, with the upper profile an arciform line. The mastoidal processes are usually small, as are the paroccipitals. The auditory bullae are quite large, but flattened or only weakly inflated, usually without a septum. The alisphenoid canal is absent. The orbit is large, and the temporal fossa is of great size.

The second upper molar is absent. The complete dental formula is $I\frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{1}{2}=38$. This formula is not encountered in all species of the family (developed in martens, *Martes*; wolverine, *Gulo*; badgers *s.s.*, *Meles*, *Helictis*, *Arctonyx* and others). A reduction in tooth number often occurs in the premolars and molars.

This occurs in various combinations $\left[I \frac{3}{3} C \frac{1}{1} \right] P \frac{4}{3} M \frac{1}{2} = 36$

(otters, Lutra); $\left[I\frac{3}{3}C\frac{1}{1}\right]P\frac{3}{3}M\frac{1}{2}=34$ (polecats, weasels, Mustela, Eyra, Galictis; American badgers, Taxidea; skunks Spilogale, Mephitis) and even $\left[I\frac{3}{3}C\frac{1}{1}\right]P\frac{2}{3}M\frac{1}{2}=32$ (skunks, Conepatus) and

 $\begin{bmatrix} I\frac{3}{3}C\frac{1}{1} \end{bmatrix}$ $P\frac{3}{3}$ $M\frac{1}{1}$ = 32 (ratel, *Mellivora*). In one case (sea otter, or *kalan*, *Enhydra*), reduction occurs in the number of incisors retained, and the formula takes the form $I\frac{3}{2}C\frac{1}{1}P\frac{3}{3}M\frac{1}{2}$ = 32. The greatest reduction, however, is reached in the number of molars and premolars $\begin{bmatrix} I\frac{3}{3}C\frac{1}{1} \end{bmatrix}$ $P\frac{2}{2}M\frac{1}{1}$ = 28 (*Lyncodon*). In rare cases, all or some of the premolars are absent, and the dental formula significantly varies individually, with age, as well as geographically—the dental formula may be $P\frac{4}{4}P\frac{3}{4}P\frac{4}{3}P\frac{3}{3}$ = 38 = 36 = 34 (badger, *Meles meles*)¹.

The fourth upper premolar and first lower molar are developed in the form of typical carnassial teeth. The upper carnassial tooth usually has three roots; its inner is well developed. The main outer cusp is not divided. The large cheek teeth, at least along the outer margin, are sharply pointed (the inner cusps are blunt) or have blunt tips and tubercules. In the first case, the posterior teeth are

¹Some contradictions in information on dental formulae of the different genera, which are often found in review works, may in part be explained by this situation.

usually elongated with an inner heel and in the second—they are strongly broadened, irregularly triangular or irregularly quadrangular in form.

There is an os penis, usually thin and long, sometimes strongly curved, divided at the end, and without a longitudinal groove. Anal glands are well developed, sometimes very strongly so, and always have a sharp, sometimes stupefying odor, especially in those forms which are able to exude secretions (skunks and, to lesser extent some badgers).

The head is usually small or of moderate length, ears are rounded, rarely quite large, but usually small and sometimes strongly reduced and fusing [with the trunk] (in the aquatic forms). The tail is of moderate length, sometimes long, considerably longer than the hind foot, and even more than half the body length; thin or more or less broad and muscular, with a wide base; in several, it is very short, only slightly extending beyond the dorsal fur. The eyes are of moderate size; but in some, they are relatively large and bulging. The tip of the nose is bare, the lips slightly movable.

The pelage, in relation to different kinds of biological types and the regions of occurrence, is quite variable. Some northern forms have a dense, soft and silky coat which is very valuable as fur (martens, sable, sea otter, or *kalan*). In the majority of aquatic forms (otters) the underfur is dense, thin and kinky overlain by coarse guard hairs. The fur of some forms is coarse and bristly, with poorly-developed underfur or without it; its value is very low.

Color is to the highest degree variable, from more or less unicolored dark brown to yellowish-red, black, white, black- and white, etc. In some cases, coloration is very bright and contrasting from black, red, yellow, brown etc. Not rarely, there are peculiar patterns on the head in the form of stripes and elongated spots. Cases of coloration, where the venter is a dark (black) color, and the dorsum a light gray or white (ratel, badger, and others) or when stripes and spots are found against the basic black background (skunks), are characteristic for the family. In some, individual and geographic variation in color is considerable.

Sexual dimorphism in color is absent, but males are usually somewhat larger than females. Age dimorphism in color is absent or is expressed only in the first juvenile pelage. Seasonal dimorphism is only manifested in northern forms and may be very sharp, with regard to length, density and other fur properties. Fur color is somewhat variable. In extreme cases, the brown summer coat may

be replaced by the white winter (ermine, weasel). There are one or two molts annually.

There are several pairs of teats (2-4), sometimes 1 (sea ofter). Concerning general appearance and body structure, the numerous species of the family are extremely diverse, although they may be divided into several biological types (see below). A feature common to all lies in their relatively short limbs. The majority are characterized by a thin and elongated body and long neck; some have a more compact and quite massive build, sometimes a heavy body; the relatively small or small and narrow head is characteristic. Among mustelids there are small forms with a very long, even serpentine body, and narrow head (no distinction between head and body)—the purely terrestrial weasels, ermines and kolonok; some are more rugged and large, but also of the polecat type; their analogs are connected with water, but less specialized minks; semiarboreal and rocky, good climbers—martens and ilka*; excellent swimmers and divers, the truly amphibious fresh-water otters with very long and flexible body. Specialization reaches its extreme degree in marine-dwelling sea otter living on the seashores, which possesses pinniped characteristics (structure of the hind limbs).

These forms with long to very long trunk and short limbs are unable to move at a trot usually move at a walk, sometimes as if "crawling" or jumping ("galloping"), with the back arched. The extremely specialized aquatic forms move poorly on land.

Another extreme type is represented by the heavy terrestrial badgers and ratel, which exhibit various degrees of adaptation to digging, sometimes high, but in any event the highest in the order. More or less "neutral" are the little specialized forms (South-Asian badgers), but the more developed are represented by the relatively large animals of low mobility with broad massive trunks (Euroasiatic and American badgers *Meles*, *Taxidea*). The skunks (*vonyuchki***) also constitute a particular category of slow-moving but small representatives of the family. This is connected with their remarkable passive defence (exuding a stinking fluid from the anal glands). The wolverine is large and massive, but a good climber.

^{*}Russian name for North American fisher, M. pennanti-Sci. Ed.

^{**}Literally, "stinkers"-Sci. Ed.

Difference in the size of the different species is very great. The largest forms attain a body length of 90 cm (badger); 120 cm (South-American otter, Pteronura brasiliensis) and even 150 cm (sea otter). The latter has a weight of up to 40 kg. The smallest 495 form has a body length of about 15 cm, a weight of about 100 g or less (weasels of the group pygmaea*—rixosa). The ratio of the size of the largest, by weight [to the smallest] is, therefore, 1:400.

All mustelids live either singly or in families; as an exception they may form small groups having a common, or neighboring, burrows. Species leading a sedentary mode of life do not occur in the family (data on some American otters are not well defined).

Trophic specialization is quite variable. There are trends toward sharply pronounced energetic carnivores feeding on warmblooded vertebrates (chiefly rodents—weasels, polecats, etc.) and strongly restricted ichthyophages (otters). With one or another defined conditions, the food of both groups may be mixed with other animals, and sometimes also plant foods. Carnivorous "collectors" constitute quite a large group, feeding on small warm-blooded and cold-blooded vertebrates and on invertebrates, often digging them out of the ground (badgers, skunks and others). There are also carnivores which hunt large animals (wolverine-deer, moose) and even a form specializing in feeding on sea-urchins (sea otter, or kalan). As a rule, they are sedentary, sometimes very firmly attached to a place. They usually construct their personal underground shelters, which sometimes have very complicated structure. and inhabit them for many years; sometimes they occupy foreign burrows. Some northern forms hibernate (common and American badgers, skunk). The number of young differs in various groups from 1-2 and up to 10.

They are mainly nocturnal, but a portion are crepuscular forms. Of the sense organs, hearing is, apparently, the most developed, and in some, smell also. The general level of psychological [mentall activity is, apparently, lower than in species of the wolf and bear families. In particular, with few exceptions (otters), they are not easily domesticated and trained. They are definitely found in all landscapes—from tundras to deserts, in humid tropical forests, marshes, rivers and sea coasts. In a vertical direction, they are distributed from depressions below sea level to extreme heights.

^{*}Spelled pygmea in Russian original-Sci. Ed.

Their geographical distribution is very extensive—nearly the entire world. The range includes the entirety of the South American continent. Central and all of North America, including the whole Arctic archipelago. In the western hemisphere, representatives of the family are absent only on the Falkland and Galapagos islands, on all islands of the West Indies and on some islands in the Bering Sea (Saint Lawrence, Hall, Saint Matthew, Nunivak); the Aleutian and Pribilof islands are included in the range. In Greenland, the range area occupies only the very northern part of the island east of Ross Strait and its eastern coastal zone southward, somewhat more southerly than latitude 70° N, lat. (below Scoresby Sound). In the Old World, the range includes the whole of Africa, Europe and the mainland of Asia. Species of the family are absent on Iceland and the majority of the Arctic Islands (Spitsbergen, Franz Josef Land, Novaya Zemlya, Severnaya Zemlya and Wrangel Island), but are encountered in Kolguev, Vaigach and the New Siberian archipelago. In the Far East, the range encompasses the Commander, Karaginsk and Kuril islands, Sakhalin, Japan, Taiwan and Hainan. In southern Asia, Ceylon [Sri Lanka], Sumatra, Bangka (absent on Belitung), Java (absent on Bali and farther east), Kalimantan and Palawan are included in the range. In the entire remaining insular region between Asia and Australia, species of the family are absent² as well as in Australia itself and the islands of the southern part of the Pacific Ocean. They are also absent in Madagascar, where the Viverridae are very richly developed.

In connection with their direct persecution (as valuable furbearing species) or exclusion from cultivated regions, the ranges of some forms were quite strongly changed. However, the range of the family as a whole has not changed substantially in the last century.

In spite of its species richness and especially its diversity of forms, the family represents a well separated group. It is distinctly demarcated from other families within the order and in the group Canoidea, and its independence does not admit of any doubt. On the whole, these are predators of quite highly, often very highly specialized type.

²Information from several authors (Weber, 1928; Hilzhelmer, 1930 and others, and even Pocock, 1941) on the distribution of the family eastward to the Philippines (otters), is apparently erroneous (Carter, Hill and Tate, 1946).

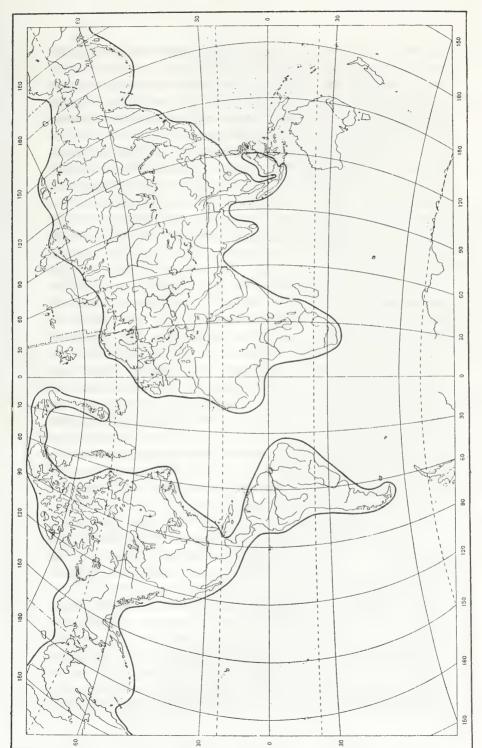


Fig. 184. Range of family of martens [weasels], Mustelidae. V.G. Heptner.

In their extreme forms they are only inferior to the cats—the most definitively predatory of the mammals. On the whole, in their group Canoidea, they are analogous to the viverrids among the group Feloidea, and are in general not inferior to them in their degree of specialization, and in some respects (adaptation to aquatic life), considerably superior to them. Among the viverrids, only one genus—Nectogale—is analogous to otters though not more specialized. The external similarity of some forms of the family with individual contemporary viverrids represents only convergence—systematically, both families are quite strongly divergent and belong to different groups (see characteristics of the order). Within the scope of contemporary carnivores, the marten family is closely related to raccoons (Procyonidae) and is relatively far from the bear and wolf families.

The family itself represents a quite ancient group—its first representatives were found in the early Oligocene together with the most primitive representatives of the wolf, viverrid and cat families. They exhibit the greatest closeness to primitive forms of the wolf family. However, differentiation of the mentioned families was, in the lower Oligocene, still not completely determined, and views concerning the most ancient and primitive forms of the marten family are contradictory (Stenoplesictinae are on one hand assigned to Mustelidae, on the other, to Viverridae). Oligocene representatives of the family were small animals, true predators with sharp teeth, apparently, like the polecat or marten. Differentiation of the main existing branches is already occurring in the upper Oligocene (otters), middle (badgers) and upper (skunks) Miocene and middle Pliocene (wolverines).

The development of the family proceeded, apparently, mainly in the northern hemisphere—in North America and Eurasia the Mustelidae were known from the lower Oligocene, in Africa they are found from the middle Pliocene, and in South America—only in the Pleistocene.

Concerning internal structure, the contemporary family is extremely varied, and until now, there has been no accepted and really satisfactory division of it into subfamilies or in general, suprageneric groups. Even long ago, division into two subfamilies was held by many authors (Mustelinae and Lutrinae—otters on one hand, and all others on the other), which division is still accepted by many; into 5 subfamilies (see below) and even into 15 (Pocock,

1922). The latter is, naturally, unacceptable, but shows well the diversity of forms, the diversity of characters and complexity of radiation in the family. The view has even been expressed that the present Mustelidae does not comprise a phylogenetically united group, but is of polyphyletic nature. The heterogeneous character of the group becomes even clearer if fossil forms are taken into account; if the extreme subdivision of existing forms (15 subfamilies) is followed, not less than 15 extinct subfamilies must also be accepted (Simpson, 1945).

It is most probable, that the most natural division of the family will turn out to be into two subfamilies—separation of otters, Lutrinae, which are very completely isolated from remaining mustelids. However, at present, until there is a full analysis of the question, it is practically more suitable to divide the family into 6 subfamilies—the extinct Leptarctinae and 5 contemporary ones. It is usually considered that there are 76 genera, of which 47 are extinct and 29 existing. This constitutes 38% of the total number of genera in the order and 22% of the existing genera. The actual number of existing genera is, however, somewhat less (see below).

The subfamily of true weasels, Mustelinae, includes the following genera³: Mustela (polecats, ermines, etc.—Eurasia, North and South America; 15–16 species); Martes (martens, including kharza [yellow-throated marten] Charronia—Eurasia; North America; 6–8 species); Vormela (marbled polecats—Eurasia; 1 species); Eira (tayra—North and South America; 1 species); Galictis (grison, including Grisonella—North and South America; 2 species); Lyncodon (South America; 1 species); Ictonyx (African polecat—Africa; 2–3 species); Poecilogale (Africa; 1 species); Gulo (wolverine—Eurasia and North America; 1 species).

The subfamily of honey-badgers, Mellivorinae, includes one genus *Mellivora* (Africa, Asia; 1 species).

The subfamily of badgers, Melinae, comprises the following genera: *Meles* (Old World badgers—Eurasia; 1 species); *Arctonyx* (hog badger—eastern Tibet and southeastern Asia; 1 species);

³The following list of genera is not in accord with data of Simpson (1945). His revision based on various data led to reduction in the number of genera, mainly by transferring some to the rank of subgenus. It is apparently possible that further reduction will take place. Genus *Grammogale* Cabrera (Cabrera, 1940, 1957), not recognized by Simpson, is here set aside. The number of species established from different sources, cannot be considered precise. Actually, they are probably somewhat fewer.

498

Taxidea (American badger—North America; 1 species); Melogale, including Helictis ("polecat" [ferret] badgers—southern Asia; 4 species).

The subfamily of skunks, or *vonyuchek*, Mephitinae, includes the genera: *Mephitis* (North America; 2 species); *Spilogale* (North America; 2–3 species) and *Conepatus* (North and South America; 7 species).

The subfamily of otters, Lutrinae, includes the following genera: Lutra (including Lutrogale, true otters—Eurasia, African, North and South America; 10 species); Pteronura (giant otters—South America; 1 species); Aonyx (including Amblonyx; "clawless" otters—Africa, Asia; 2 species); Paraonyx (Africa; 3 species); Enhydra (sea otter, or kalan—northern Pacific Ocean; 1 species). In the entire family, therefore, there are 24 genera and about 70 species. This constitutes about 1/3 of the species of the order. It is more probable that there are about 65 species. As regards the number of genera and species, the family is the richest one among the group Canoidea, and one of the richest in the order. It is only inferior to the viverrids (about 36 genera and 75 species) and greatly exceeds the number of the species of wolves and cats.

Of the total number of genera of the family, four are African (not counting Mustela, which penetrates to the northwestern edge); six are Asian and Eurasian, three-North American, two-South American (Grammogale is not taken into account); 2—Afro-Asian, 3—North and South American: 1—distributed in Eurasia, North and South America; and 1-in Eurasia, the Americas and Africa. Therefore, as regards the number of genera, the fauna of the Old World and especially of Asia is the richest and most heterogeneous. As regards the number of species, the poorest is shown to be the fauna of North America (5 endemic species and several common to the other continents), and the richest—Eurasia (about 17 endemic species and several others common to the America and Africa). It is remarkable, that in spite of only two endemic genera, both monotypic, the fauna of South America is relatively rich in species (about 16), mainly on account the diversity of otter species and skunks of the genus Conepatus.*

The practical significance of the family is very great. It is one of the most important, if not the most important, group of carnivores. The species of the family play a particular great role as

^{*}In Russian original, misspelled Canepatus-Sci. Ed.

fur-bearers. If the chinchilla is not counted, the family comprises the most valuable fur-bearing animals of the existing fur species—martens, fisher, otters, and most of all, sable and sea otter (kalan). Some of them have even played a great historical role—the opening up of Russian Siberia was first of all connected with sable, whereas the northern Far East and the shore of the northern part of the Pacific Ocean, including the American—with sea otter. The penetration of Europeans into northern North America from the south, was also determined chiefly by furs, among which an important role was played by American sable [marten], fisher and mink. Exploitation of mustelids played an important role in the life of natives of northern Eurasia and America, and the importance of sable in ancient Russia and to present times is generally known. Representatives of the family play one of the chief roles in the economics of the fur trade at the present time.

Beside the particularly valuable species mentioned, there are a considerable number of other less expensive species, but which are obtained in large quantities such as polecats, ermine, Siberian weasel, mink, wolverine, pama*, various otters, etc., which give very large amounts of fur every year. Otters themselves represent the main fur species in tropical and equatorial countries which, owing to their natural conditions, are very poor in fur-bearing animals. There are some less valuable fur-bearing species (badgers, etc.) which, in total, also play a certain role. Finally, the very great, and at the present time, the main product of fur farming consists of American mink raised in various, artificially obtained color forms (mutations). The mink is now a more important fur-producing animal than the silver-black fox. Sable, martens, and skunks are also raised in captivity, but their importance is very small.

Many species specializing in feeding on small rodents (weasels, ermine, polecats, and others) are themselves considered important regulators of agricultural pests, and of reservoirs and carriers of dangerous infections (plague and others). Otters play a known role in their capacity to exterminate fish and cause harm to fish-farming. Finally, a few species serve as objects of sport hunting. The fat of some is used in folk medicine.

In the fauna of the USSR are represented 4 out of 5 subfamilies (80%), 8 of 24 genera (33%) and 17 species (not counting acclimatized) of 70 (about 23%) (V.H.).

^{*}Meaning unclear-Sci. Ed.

Key for Identification of Genera of the Family Mustelidae

- - 2 (1). Digits of the fore and hind limbs are not conjoined and movable (sometimes perhaps connected by membrane), hind not forming flippers and middle digit [III] is longer than others. In lower jaw, 3 incisors on each side, molars and posterior premolars with well developed pointed tubercles or with sharp cusps.
- 500 4(3). External ear conch present, color of one sort or another.

 Molars and premolars 5-6 in lower jaw.
 - 5 (6). Ventral surface of body black or blackish-brown, dorsal light, dirty-gray (without yellow color). Posterior upper molar 2–3 times larger than preceding one. Body length more than 60 cm genus of badgers, *Meles* (page 1228).
 - 6 (5). Color different, if ventral color black or darker than dorsal, then back has a clearly developed yellow or yellowish tone. Posterior upper molar not larger than preceding one.
 - 7 (8). Digits united by broad membrane which is nearly completely devoid of hairs, on hind foot extending to claws. Soles of fore and hind feet bare below. Tail long (not less than half length of trunk with head), base broad and muscular. Dimensions large—body length about 70–75 cm. Last molar tooth approximately equal in dimensions

⁴Crown viewed from above.

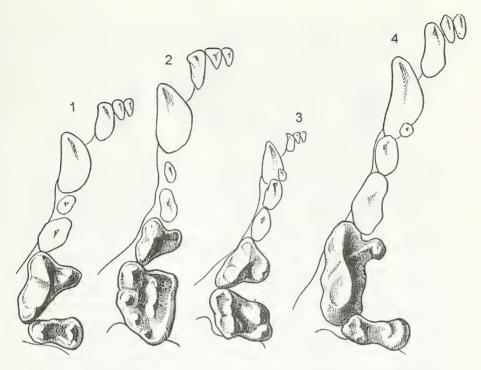


Fig. 185. Characteristic structure of posterior part of toothrow in upper jaw of some genera of the weasel family, Mustelidae. Sketch by N.N. Kondakov:

1—Genus of honey-badger, Mellivora; 2—Genus of badger, Meles; 3—Genus of otters, Lutra; 4—Genus of wolverine, Gulo.

to preceding one. First upper premolar pushed away from toothrow and lies at inner side of canine (Figure 186) genus of otters, *Lutra* (page 1283).

- 8 (7). Swimming membranes between digits absent, or are very weakly developed, covered with hairs and do not reach end of digits. Food pads*, at least those between digits, with hair. First upper premolar lies posterior to canine. Tail of different lengths, but not muscular and base not broadened.
- 9 (10). Dimensions are large—body length more than 70 cm, condylobasal length of skull more than 130 mm. Tail relatively short (about 20 cm). Coloration evenly brown with light bracket-form bands of different intensity



Fig. 186. Position of canine and first premolar of the upper jaw of representative of genus of otters, Lutra. Sketch by N.N. Kondakov.

passing along sides and across croup from shoulder to shoulder genus of wolverines, *Gulo* (page 920).

- 10 (9). Dimensions smaller—body length less than 65 cm, condylobasal length of skull less than 115 mm. Tail length variable; coloration otherwise.
- 11 (12). In upper jaw behind canine 5 teeth (4 premolars and 1 molar), in lower—6 (4 premolars, 2 molars). On posterior side of main cusp of last premolar (third tooth from rear) the lower jaw has a small additional cusplet (Fig. 187)genus of martens, *Martes* (page 749).



Fig. 187. Last lower premolar tooth of genus of martens, *Martes* (sable, *Martes zibellina* L.) with additional cusplet on main cusp. Sketch by N.N. Kondakov.

- 12 (11). In upper jaw behind canine, 4 teeth, in lower—5. Additional cusplet on posterior side of last premolar (third tooth from behind) of the lower jaw absent.
- 13 (14). Back is parti-colored—yellow with irregular dark spots and stripes, or dark, densely covered with irregular light spots and stripes. Posterior processes of pterygoids reach tympanic bullae and united with them (Fig. 188) genus of marbled polecat, *Vormela* (page 1176).
- 14 (13). Coloration otherwise, without spots or stripes. Processes of pterygoids do not reach tympanic bullae genus of ermines and polecats, *Mustela* (page 954) (V.H.).

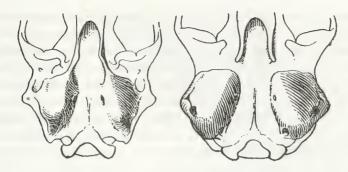


Fig.188. Position of pterygoid processes in genus *Vormela* (joined with tympanic bullae) and in the other genera of the weasel family (not joined with tympanic bullae—black [common] polecat, *Mustela putorius* L.). Sketch by N.N. Kondakov.

502

Subfamily of Weasels

Subfamilia Mustelinae Gill, 1872

Genus of Martens

Genus Martes Pinel, 1792

- 1775. Martes. Frisch. Natur-Syst. d. vierfüss. Thiere, p. 11. According to decision of the International Commission on Nomenclature, names in this edition have no nomenclatural significance.
- 1792. Martes. Pinel. Actes Soc. Hist. Nat. Paris, 1, p. 55. Martes domestica Pinel = Martes foina Erxleben.
- 1829. Zibellina. Kaup. Entw. Gesch. u. Natur. Syst. Europ. Thierw., 1, p.p. 31, 34. Mustela zibellina Linnaeus.
- 1865. Charronia. Gray. Proc. Zool. Soc. London, p. 108. Mustela flavigula Boddaert.
- 1928. Lamprogale. Ognev. Memuary Zool. otd. Obshch. lyubit. estestvozn., 2, p. 26. Substitute for Charronia Gray, 1865, preoccupied by Charonia Gistel, 1848. (Mollusca). (V.H.). Species of moderate dimensions.

Skull relatively narrow and elongated, without sharp crests and protuberances. Braincase relatively quite large. Facial portion relatively elongated, zygomatic arches weak, not strongly diverging, laterally interorbital and postorbital constrictions weakly defined.

Supraorbital processes small. Upper profile of skull gently sloping, slightly convex. Convexity of fronto-nasal region at level of infraorbital foramena weakly developed. Diameter of infraorbital foramena almost equal to diameter of alveolus of canine. Bony auditory bullae are quite large and their inner parts noticeably bulging towards one another. Hamate processes of pterygoid bones not united with auditory bullae. Mastoid processes small, weakly protruding laterally, lateral occipitals (paroccipitals) well developed. Bony palate wide.

Dental formula
$$I = \frac{3}{3} C \frac{1}{1} P \frac{4}{4} M \frac{1}{2} = 38$$
.

First premolars very small and sometimes shed, but an alveolus or its traces remains. On main apex of last lower premolar (anterior to carnassial tooth—third tooth posteriorly), there is a small additional cusp on the inner side. On inner side of median apex of lower carnassial tooth (first molar—second tooth posteriorly) there is no additional cusplet. Well developed pointed apex on inner blade of upper carnassial tooth (P4).

Trunk is elongated, but not to an extreme degree, or moderately short—general body structure fairly slender and relatively proportional. Tail quite long—in various species from 1/3 to 2/3 of body length. Head comparatively large with large protruding ears, broad at base, almost triangular in form, facial part pointed. Large ears and sharp muzzle give head a short, broad wedge-shaped form—characteristic of "marten" appearance. Limbs digitigrades—fore- and hind feet broad.

Fur dense, long, soft and silky (one of the most valuable furs). Tail covered with long hairs, fluffy. Color, in majority, is unicolor brown tones; in one case it is bright and patchy, with a combination of white, black, yellow and brown. On the throat and chest, there is usually a lighter area.

503

Seasonal dimorphism in character of fur very pronounced; in winter, soles of the fore- and hind feet are entirely or almost entirely covered with dense hairs. Seasonal variations in color slight. Sexual differences in color are absent; but dimensions of males average larger than females, and in several forms are quite considerable; sometimes (M. pennanti) sexual differences exist in fur characters (fur of females is softer and finer and, consequently, more expensive than that of males).

There are two pairs of inguinal teats (subgenus Martes).

All martens are very active, quick, flexible and clever animals. All are adapted not only to a terrestrial, but also to an arboreal mode of life, some to a very complete degree (able to descend head first down a trunk, their hind feet capable of being turned backwards, etc.). Because of their relatively short limbs, they move on land by jumping, with their back arched. They are forest and montane-forest animals, also inhabiting unforested mountains; however, they do not live in extremely high mountains (nival zone). They are strictly sedentary, and monogamous. Litters from 1-2 and 3-4, up to 8. Shelters are mainly in hollows and in tree trunks, but also in rock clefts. They are solitary animals. They are predators, feeding on flesh, chiefly of small rodents, but sometimes also on larger warm-blooded animals, even small ungulates (yellow-throated marten). They also utilized lower vertebrates and invertebrates, and in the ration of several, a significant role is played by plant food (berries, nuts). Torpor or hibernation does not occur.

In dimensions, the species of this genus are quite homotypical. The majority have a body length of about 40–50 cm and a weight of up to 1800 gm. Two species are large—the yellow-throated marten, *M. flavigula*, has a body length of about 75–80 cm and a weight more than 2.5 kg, and the fisher, *M. pennanti*—a body length of about 70 cm and a weight up to 6 kg.

The range of the genus is vast and covers a considerable part of the temperate and cold-temperate zones of the northern hemisphere, part of Central Asia and the region of subtropical and tropical forests of southeastern Asia. It occupies all of Europe, the greater part of Asia, and the northern half of North America. In Europe and Asia the range extends from the northern limit of forests [southward] to Spain, Italy, Greece, Crete, Asia Minor, Syria, Palestine, Iran, West Pakistan, Kashmir, Punjab, Himalayas, Indochina, the Moluccas, Sumatra, Banka [Island], Java and Kalimantan (Borneo). A small part of the range, in southern India, is cut off from the general area of habitation (for details, see below under descriptions of individual species).

In North America, the range in the north is limited by the northern border of forest vegetation. The southern border is represented by a meandering line, extending from the Atlantic coast westwards through the states of Connecticut, New Jersey, Virginia, northern North Carolina and Tennessee, Indiana, northern

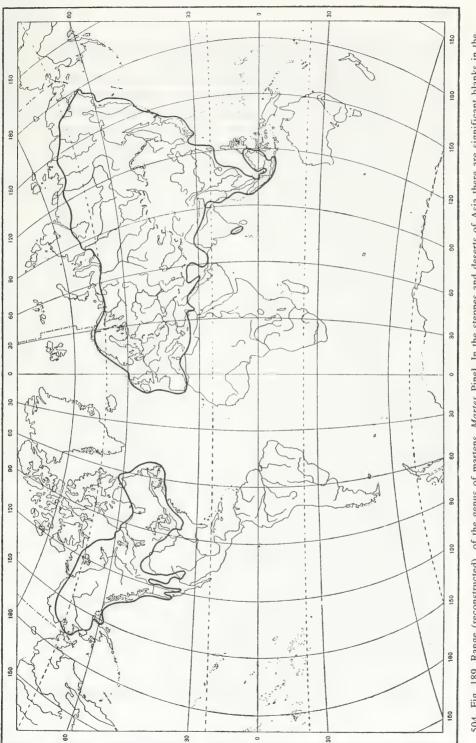
Illinois, northeastern Iowa and Minnesota (except the southwest). northeastern North Dakota, the southern part of Saskatchewan and the southeastern corner of Alberta. The range occupies all of British Colombia and from there and from Alberta, the range gives off two large extensions southward along montane regions. One extends along the coastal regions-along the western parts of the states of Washington, Oregon and to the central parts of California, and the other, more deeply into the region, extending along the eastern borders of the states of Washington and Oregon to Idaho, the western parts of Wyoming into Utah, Colorado and to the northern parts of New Mexico. In the range is included Newfoundland, Cape Breton Island, Vancouver, the Queen Charlotte islands and others along the Pacific coast of America northward to 60° N. lat. (absent on Kodiak and the Aleutian islands). In sketching the boundaries in the steppe and desert regions of Asia, considerable gaps exist in relation to natural conditions; in Siberia, the range is considerably changed in some places due to human activity: there are blank areas and the northern border does not correspond everywhere to the restored range cited.

Within the limits of the family, the genus itself constitutes a well-isolated group, characterized by a series of features, most of all, by the dental formula. Craniologically, the genus is entirely uniform and the species within this category of features are characterized basically in details. The genus is well delimited from closely related genera, in particular *Mustela*. The uniting of these genera is a former matter. It is an entirely whole group, not only in relation to its morphology, but also in an ecological and zoogeographical sense. At present, the independence of this genus is not doubted.

Moreover, attempts to divide the true martens, united here in the genus *Martes*, into a separate subfamily Martinae, which were done in the past, and which made sense only in the case of extreme subdivision of the family, cannot be considered established, and are now rejected.

Many authors divided the genus into two—the genus of true martens (our martens and the American, and sable), *Martes*, and that of the yellow-throated marten, or Himalayan marten, *Charronia*. According to a series of characteristics the yellow-throated marten is sufficiently well differentiated from the true martens; however, it is more correct to separate it only as subgenus. There are no essential craniological differences in the yellow-throated marten.

505



504 Fig. 189. Range (reconstructed) of the genus of martens, Martes Pinel. In the steppes and deserts of Asia there are significant blanks in the range. The range of the genus in America coincides with that of the American marten (American sable), Martes (Martes) americana Turt. V.G. Heptner.

Therefore, in the genus are two subgenera—Charronia with species and Martes, comprising all the remaining.

The determination of the position of this genus within the limits of the family, given the diversity of its radiation, is quite difficult. This group is, in some respects, highly specialized. However, with respect to the relative completeness of the dental system, it may be conditionally placed at the beginning of the series of genera of the family, and of the subfamily Mustelinae.

Concerning its origin, *Martes* belongs to a number of primitive genera of the subfamily; fossil representatives of the genus are known from the lower Pliocene (according to some data—from the Miocene) of Europe and Asia. The closeness of the connections between the primitive forms are not clear—starting from the lower Oligocene, a quite large number of genera of the subfamily are known, mainly from the Miocene. In particular, the genus *Mustela*, to which the genus *Martes* is quite close, is known from the upper Miocene.

The number of the species in this genus is not yet fully established; usually eight are admitted⁵: sable, *M. zibellina*; Japanese sable, *M. melampus*; pine marten, *M. martes*; American marten, *M. americana*; stone marten, *M. foina*; ilka (fisher-marten or pekan), *M. pennanti*; kharza [yellow-throated marten], *M. flavigula* and South Indian kharza, *M. gwatkinsii*.

The actual number of the species is, apparently, less, not more than 6. *M. melampus* is only a subspecies of *M. zibellina*, and *M. gwatkinsii* is only a race of *M. flavigula*. *M. americana* is closely related to the sable and to the pine marten, which, in their turn, are very closely related to each other. The relationship between these species requires further clarification. The 6 species of the genus constitute about 8.5% of the species of the family and 17–20% of the species of the subfamily.

The greatest number of species are endemic to Eurasia (4). In America, there are two: the fisher, *M. pennanti* and the American marten, *M. americana*.

Both in Eurasia, as well as in America, this genus has great practical significance, since in it are included very valuable furbearing species—all true martens and among them, the sable. The importance of the yellow-throated marten in this respect is not great. The *kharza* plays some role as a destroyer of game animals,

⁵Reference to 10 species in the genus (Novikov, 1956), is evidently based on the value of such "split" species, as in Miller (1912).

and in Europe the martens—the pine and in particular the stone—cause harm to the hunting economy and to poultry enterprises.

In the USSR are found 4 species: 3 of the subgenus Martes: 1) sable M. zibellina Linnaeus, 1758; 2) pine marten, M. martes 506 Linnaeus, 1758; 3) stone marten, M. foina Erxleben, 1777, and one of the subgenus Charronia: 4) yellow-throated marten, M. flavigula Boddaert, 1785. They constitute 66% of the species of the genus and about 1.2% of the fauna of the country.

Species of this genus are distributed over the entire forest zone of the Union and in the mountains of the Caucasus, Middle Asia and southern Siberia.

They are valuable fur-bearing species (V.H.).

Key for Identification of Species in the Genus Martens

- 2 (1). Coloration uniform—reddish-brown or brownish; a light spot may exist, on throat and chest only, white, yellowish or bright-yellow color, or head may be lighter than body, sometimes even whitish. Tail length comprises less than 2/3 of body length. Dimensions small—condylobasal length of skull not more than 90 mm, adult body length not more than 60 cm.
- 4 (3). Tail relatively long. Its length with terminal hairs more than half the body length—it extends beyond the ends of

the extended hind limbs for more than 1/4 of its length. Throat spot variable in form, but well-defined and with sharp outline. Top of head same color as that of back.

Auditory bullae shorter and widely separated. Distance between them at middle of their length more than half of distance from anterior point of bulla and posterior margin of lateral occipital process.

5 (6). Throat spot color pure white and usually gives off two posterior projections extending to the forelimb. Inner part of upper molar is not wider or only slightly wider than the outer (Figure 190). Tapering, posteriorly pointing projection along posterior border of sphenopalatine notch absent, or it is barely noticeable. In winter pelage, a bare, spotted pad is observed among the hairs on sole, and sometimes digital pads⁶ stone marten, *M.* (*M.*) foina (p. 874).

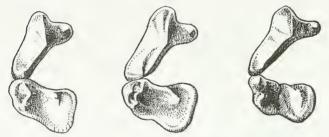


Fig. 190. Last premolar (carnassial) tooth and first molar of upper jaw of sable (left), Martes (Martes) zibellina L., pine marten, Martes (Martes) martes L., and stone marten, Martes (Martes) foina Erxl. Sketch by N.N. Kondakov.

6 (5).* Throat spot varies from light-yellow to orange, rarely white; usually spot gives off posterior projection between forelimbs.

Inner part of upper molar considerably wider than outer. Well-marked posteriorly pointing projection usually found on posterior border of sphenopalatine notch. In winter pelage the digital pads on soles hidden in hairs forest marten, *M. (M.) martes* (p. 825) (V.H.).

⁶Differentiation between stone and pine martens by form and color of throat spot, though most frequently practiced, is not always reliable (see section below "Description" of species). For purposes of identification, characteristics of teeth structure are essential.

507

^{*} In Russian original, "5(5)"-Sci. Ed.

Subgenus of True Martens

Subgenus Martes Pinel, 1792

SABLE

Martes (Martes) zibellina Linnaeus, 1758

- 1758. *Mustela zibellina*. Linnaeus. Syst. Nat. Ed. X. 1. p. 46. Northern Siberia. According to Ognev (1931) and other authors, more precisely: western Siberia north of Tobol'sk.
- 1840. Mustela melampus. Wagner. Schreb. Säugeth. Suppl., 2, p. 229. Japan.
- 1844. *Mustela brachyura* Temmink. Siebolds Fauna Japon. Mamm., p. 33. Japan, Hokkaido.
- 18557. Mustela zibellina var. asiatica. Brandt. Mém. mathem., phys. et natur., 7, p. 6, 23, Taf. 1, Fig. 1. Kamchatka.⁸
- 1855. *M. zibellina* var. *alba*. Brandt. Ibidem, p. 14, Taf. 2. Fig. 5.
- 1855. *M. zibellina* var. *fusco-flavescens*. Brandt. Ibidem, p. 14, Taf. 2, Fig. 6, Taf. 3, Fig. 7.
- 1855. M. zibellina var. ochracea seu ferruginea. Brandt. Ibidem, p. 14. Taf. 3, Fig. 7.
- 1855. *M. zibellina* var. *maculata*. Brandt. Ibidem, p. 14, Taf. 3, Fig. 9.
- 1855. Mustela zibellina var. asiatica rupestris. Brandt. Ibidem, Taf. 2, Fig. 2.
- 1855. Mustela zibellina var. asiatica sylvestris. Brandt. Ibidem, Taf. 2, Fig. 3.
- 1918. *Mustela zibellina subsp. kamtschadalica. Birula. Otchet devatel'nosti Ross. Ak. Nauk, p. 82. Kamchatka.

⁷Date for individual volume—collection of works reprinted from volume VII of the "Memoirs" (see list of references at end of book). The pagination is given according to the same edition.

⁸In the work of Brandt mentioned, the individual or "ecological" (mountain, forest) trends of the sable are described. By the name, "var. asiatica", Brandt means all Asiatic sables in contrast to American sables ("var. americana"). At the same time, in Table 1, Fig. 1 is illustrated a normally colored sable, originating, as stated in the legend from Kamchatka. Formally, under such conditions, the name asiatica may be ascribed to Kamchatka sables. However, since in the whole sense of the paper it is clear that Brandt under his var. asiatica had all Asian sables this cannot be done.

*In Russian original, not in chronological order—Sci. Ed.

- 1922. Mustela zibellina princeps Birula. Byalynitskii-Birula. Ezheg. Zoologich. muzeya. Ross. ak. nauk 1917–1921, 22, p. 8. Barguzin range.
- 508 1922. *Mustela zibellina* var. *kamtschatica*. Dybowski. Arch. Tow. Nauk. Lwowe, 1, p. 349, Nomen nudum. Kamchatka.
 - 1922. Mustela zibellina var. baicalensis. Dybowski. Ibidem, p. 349. Nomen nudum. Vic. Baikal.
 - 1922. Mustela zibellina var. amurensis. Dybowski. Ibidem, p. 349, Amur, Ussuri.
 - 1923. *Mustela melampus coreensis**. Kuroda et Mori. Journ. Mammal. 4, p. 27. Tenan, South[ern]. Chusei distr[ict]. Korea.
 - 1925. Martes zibellina yeniseensis. Ognev. Journ. Mamm. 6, No. 4, p. 277. Krasnoyarsk u[yesd], Yenisei guber[naya], taiga plain.
 - 1925. Martes zibellina sajanensis. Ognev. Ibidem, p. 278. Orzybai [=Orsyba] river, northern Sayan [mountains].
 - 1925. Martes zibellina sahalinensis. Ognev. Ibidem, p. 279. Sakhalin, Vedernikovo. [=Saghalien, Wedernikovo].
 - 1927. *Martes zibellina correensis*. Kishida. Choju Chosahokoku, 4, p. 130. Korea.
 - 1927. Martes zibellina hamgyensis. Kishida. Dobuts Zasshi, 39, p. 509.**
 - 1941. Martes zibellina tungussensis. Kusnetzov. Tr. Mosk. zootekhnich. inst., I, p. 116. Lower Tunguskaya [river].
 - 1941. *M.*(artes) z.(ibellina) sahalinensis arsenjevi. Kusnetzov. Ibidem, p. 122. Samarga River, Ussuri Territory.
 - 1941. *M.(artes) z.(ibellina) sahalinensis schantaricus*. Kusnetzov. Ibidem, p. 122. Bolshoi [Great] Shantar Island, Okhotsk Sea.
 - 1943. ⁹Martes zibellina averini. Bashanov. Bazhanov. Kazakhskii fil. Ak. N. Souza SSR in 1942, p. 13. Katon-Karagaiskii region, Vostochno-Kazakhst. obl[ast], southern Altai.
 - 1947. Martes zibellina altaica. Jurgenson. Yurgenson. Tr. Pechoro-Ilychskovo*** Zapov. 5, p. 179. Oirotskaya auton. obl[ast], Altai. 10

***In Russian original, misspelled "Ylychskovo"-Sci. Ed.

^{*}In Russian original, misspelled koreensis-Sci. Ed.

^{**}No type locality cited in Russian original-Sci. Ed.

⁹Released apparently, in 1944.

¹⁰Type (Zoological museum, Moscow university) from left bank of middle course of Bystrukha river, upper Katun [river]; southwestern Altai (V.H.).

- 1955. Martes zibellina tomensis. Timofejev et Nadejev. Timofeev et Nadeev. Sobol', p. 37. Kuznetskii Alatau. Tutuyas river—tributary of Tom [river].
- 1955. *Martes zibellina angarensis*. Timofejev et Nadejev. Timofeev et Nadeev. Ibidem., p. 41. Angara valley in Boguchaev region, Krasnoyarskii territory.
- 1955. Martes zibellina ilimpiensis. Timofejev et Nadejev. Timofeev et Nadeev. Ibidem., p. 44. Kochechumo watershed—tributary of Kotuya [river], 67° N. lat. (about 100° E. long.).
- 1955. Martes zibellina vitimensis. Timofejev et Nadejev. Timofeev et Nadeev. Ibidem., 47. Valley of the Mama river, right tributary of the Vitim [river], Yakutiya.
- 1955. *Martes zibellina obscura*. Timofejev et Nadejev. Timofeev et Nadeev. Ibidem., p. 47. Upper Chikoi river—right tributary of Selenga [river], Trans-Baikaliya.
- 1956. "M.(artes) M.(artes) z.(ibellina) jakutensis. Kusnetzov (1941)". Novikov Khishchnye mlekopitayushchie fauny SSSR, p. 185. Yakutiya, Aldan Valley¹¹ (V.H.).

509 Diagnosis

Tail length with terminal hairs not more than half the body length. Color uniform, on throat and chest a yellow spot of irregular form; sometimes absent. Head usually lighter than back, sometimes whitish. Bony auditory bullae relatively elongated and adjacent. Inner half of upper molar is wider than outer (V.H.).

Description

The sable, in its winter fur, is a very graceful and elegant animal. It has a moderately elongated body and relatively short limbs with

"In the referenced book by G.A. Novikov [1956; see Lit. Cit.], the "Yakut sable" was designated as that set forth in quotation marks. Nevertheless, in the work of B.A. Kuznetsov (1941) to which Novikov refers, the Yakut sable was not given a name, and was designated as "7) Martes zibellina s. sp.? Yakut sable" (page 120). A short preliminary diagnosis was given by B.A. Kuznetsov, and it was shown that the "Yakut sable" lived mainly in the valleys of the Aldan and Kurchum rivers". Since B.A. Kuznetsov did not give a scientific name to the Yakut form, its description must be formally considered that which has been given by G.A. Novikov and must be named M. (M.) zibellina jakutensis Novikov, 1956. As for type locality, since "Yakutya" (mentioned by Novikov) is too broad and ill-defined, it is hereby restricted to the Aldan valley.

very broad, thickly furred feet. The sole pads of the digits and feet and the claws are hidden in the dense hairs. The tail is comparatively short, its length usually constituting about 1/3 of the body length and not exceeding half of its length. In the "skinned"* animal it is small (no more than 1/4 of its length) and extends slightly beyond the posteriorly extended hind legs. It is densely covered with long hairs and is very fluffy. The head of the sable appears very large, cuneate in form—the nasal part tapering, but slightly extended; the ears are large, upright, of triangular form with a broad base and a somewhat blunt tip. The eyes are bulging, quite large, black; the naked tip of the nose is black and the claws are black.

Since the trunk of the sable is elongated, and the legs are relatively short, the animal always arches its back strongly, its hind parts are often higher than the shoulder; the tail is always fluffy. Nevertheless, the sable in its winter garb, is a very well-proportioned animal, an appearance which has nothing in common with a small cat. The general impression from the appearance of the sable confirms its extraordinary activity and speed, deftness and confidence of movement. The sable runs quickly, moving by jumps ("trotting"; it almost never walks, due to the above-noted proportions of its body), it can make great jumps, can climb trees and cliffs well and can dexterously make its way among the stones, fallen trees, etc. Finally, due to its broad, densely haired feet, it can confidently traverse loose snow without sinking in. The weight load of the sable track is less than in all our other species of the genus.

The appearance of the sable in summer garb is entirely different—it looks thin and long, with longer legs and a thinner tail. The head seems disproportionately large, with huge ears, and the neck is thin and long. The relatively great breadth of the feet in the summer sable draws attention to it.

The summer pelage of the sable is short, coarse and sparse, and the underfur is weakly developed. The length of the guard hairs on the rump (croup) is 20–30 mm with a thickness of 100 to 105 microns; length of underfur is 12–14 mm with a thickness of 16–18 microns. For each guard hair there are 5–6 underfur hairs; the number of hairs in a 1 cm² area of skin on the rump is equal to 600–700.

^{*}Literally, "in flesh"-Sci. Ed.

The winter pelage of the sable is dense, with a large quantity of underfur, exceptionally fluffy and silky. The length of guard hairs on the croup equals 36-48 mm, the length of underfur, 24-28 mm. The thickness of the guard hairs is 85-90 microns, of underfur, 14 microns. Therefore, winter underfur, with a length almost double that of the summer, and are even absolutely thinner; such proportions are also true for the guard hairs. For one guard hair, there are 20-25 underfur hairs; the total number of hairs in 1 cm² area of skin on the rump is, on the average, 13,500 (Kuznetsov, 1951, Yenisei sables; Pavlova, 1951). In winter pelage the hairs of the tail are considerably longer, denser and fluffier (they reach 85 mm) and the feet are also covered with denser and longer hairs. In summer pelage the claws and pads of the digits and soles can be seen, but in winter they are completely hidden. The winter sable walks on a furry cushion. The great luxuriance of the fur on the feet in winter considerably increases the area of the feet, and facilitates the animal's movement on loose snow.

While the winter fur of the sable is entirely variable in color (see below), the summer pelage of the animals in a single locality and in various parts of the range, is uniform. Even in very light races (for example, Tobolsk sable), the summer fur is very dark.

Its color is monotone: dark-brown, darker along the back, slightly lighter on the sides, and still a bit lighter on the belly. The tail is blackish-brown. The legs have the same tone as the sides or they are somewhat darker than the color of the back. On the throat and along the lower neck, there is a lighter yellowish area with completely undefined outlines, spreading onto the sides of the neck. In some, it is absent. Between the ears and eyes, a dark area extends to the nose; the cheeks, the region in front of the ears, the ears, and behind the ears is occupied by a light area of ochreous color merging posteriorly with the lateral parts of the throat spot. This pattern is sometimes absent or weakly defined, and the whole head is darker. The ear margins are trimmed with short ochreous hairs.

The generally dark color of the summer sable is explained not so much by the coloration of the various hair categories as by the structure of the fur. The underfurs have a yellowish-brown color, the guard hairs and contour hairs are dark-brown or almost black. The previously mentioned ratio of both hair categories (5–6:1)

thus results in the general color of the fur being mainly determined by the color of the contour hairs (Pavlova, 1951).

The winter pelage is characterized by a lighter color of the underfur—bluish-gray at the base and sandy or brownish at the tips. The guard hair has the same color as in summer, but with a predominance of black pigmentation over the brown; however, the number of the down hairs for each guard hair is much greater (see above), and the general color, to a great extent, is determined by them (Pavlova, 1951). The deviations are more strongly expressed in the general tone of the color of the underfur. In this respect, in one and the same place, individual variation in color has a much greater range in winter than in summer, and geographic variation in color is considerable, and much greater than in summer.

The winter fur of the sable has a quite uniform color over the entire body. The sides and the lower surface of the body has a somewhat less intense color, but the contrast is insignificant. The tail has the same color as the back, but the terminal half is usually darker. The legs, and especially the feet, are darker than the back. The anterior part of the head and ears or the whole head is considerably lighter than the remaining parts of the trunk. On the throat and neck there is a large light area, yellowish in color, without sharp outlines.

With this type of color distribution, its general color is subjected to very great variation bearing both an individual and a geographical character. The general color tone within the species varies from sandy-yellow to brownish-black. The character of the throat patch also varies as well as head color and the degree of uniformity of color of the different parts of the body. Sables having either very monotone color, or more contrasting colors occur.

The darker color of back and tail described above is characteristic of light-colored sables—the darker the sable, the less its contrast, and in the darkest sables, not noticeable. So also with the color of the head—in the majority of cases, it is light-grayish and only in particularly dark sables is it the same color as the back; the cheeks are always slightly lighter. Sometimes, even in relatively dark sables, the head is light, occasionally almost pure white. The throat patch is very variable. In many animals, it is completely absent or only represented by a tiny, weakly colored part of the fur. Sometimes, on the contrary, the throat patch with all its variation in shape, is sharply outlined. The color of the patch is

or the other tendency in the development of the patch may also carry a geographical character.

A century of practice in the Russian fur business has elaborated a very precise categorization of color variation in sable fur. In it, no attention is assigned to the quality of the fur itself, and it is applied and adapted to all the geographical forms (sorts) of sable. These sorts are as follows:

Golovka. Color particularly dark. All fur pitch-black or blackish-brown. Guard hairs black with barely noticeable brownish tinge. Underfur dark-bluish without light hair tips. Throat patch weakly defined or has form of small orange "star". Head dark.

Skins of golovka are divided into vysokaya golovka (extra)—skin color pitch-black with almost pure black guard hairs; normalnaya golovka—skin color blackish-brown with brownish-black guard hairs.

Podgolovka. Color lighter. Spine and sides of skin dark-brown or dark-chestnut color without well-defined reddish tinges on sides. Guard hairs dark-brown or dark-chestnut. Underfur gray (blue) with chestnut hair tips. Head grayish, lighter than spine. Throat patch ill-defined, not bright.

Skins of podgolovka are divided into vysokaya podgolovka—skin color dark-brown with dark-brown guard hairs and bluishgray underfur, the hair tips of which have dark-chestnut tints; and normalnaya podgolovka—skin color dark chestnut with dark brownish guard hairs and bluish-gray underfur with chestnut hair tips.

Vorotovyi. Color medium-dark. Skin surface dark-brownish or moderately intense brownish with a dark stripe along the spine and lighter, slightly reddish sides. Guard hairs on spine dark-chestnut, sides are lighter. Underfur grayish with reddish-brownish or dark sandy-yellow hair tips. Head light, grayish. Throat patch large, bright.

Skins of *vorotovyi* sable are divided into *temnyi* [dark] *vorotovyi*—skin color dark-brownish with weakly defined reddish tinges on sides, guard hairs chestnut, underfur with reddish-brownish hair tips; and *normalnyi* [normal] *vorotovyi*—skin color brownish with clear reddish tinges on the sides, guard hairs light-brownish, and underfur with sandy-yellow hair tips.

Mekhovoi. Color light (light-brownish, sandy-yellow, or pale-yellow). Guard hairs brownish or light-brownish. Underfur

light-gray with reddish or yellowish hair tips. Head light, grizzled gray. Throat patch ill-defined, large.

With regard to all remaining qualities, the skin of the mekhovoi sable is evaluated at about 15-20%, the dark vorotovyi-at 30-35%, and the vysokaya podgolovka—at 60-65% of the value of the vvsokava golovka skin (Kuznetsov, 1952).

Golovka and podgolovka categories comprise the group of "dark" sables, vorotovvi is designated as "medium", and mekhovoi as "light". The scheme given obviously characterizes the correlation of color of different parts of the body, particularly the color tone of the head.

Amplitude of individual variation in different populations and races may differ. In several parameters the range of variations is particularly great, and the difference between the extreme forms is great.¹²

This or another percentage of relationship between basic color 512 types in different parts of the species range, with other equal conditions, well characterizes individual geographical races and populations (see below, section on "Geographic Variation"). In several races, separate types may rarely be found. Thus, in Tobol'sk sables, there are no golovka, and in some Trans-Baikal, light sables are rare, and golovka constitutes up to 70%. At the same time, the numerical ratio of color forms within one race may change from year to year, and sometimes this change is fairly considerable. The multiyear average is, however, maintained. In Tofalar region of Irkutsk district, these fluctuations had the following form (Nadeev and Timofeev, 1955) (Table 48).

Table 48. Change in the ratio of color forms within one race

Winter	Skin quality			
	Total number	Dark (%)	Medium (%)	Light (%)
1941/42	269	16.4	67.6	16.0
1943/44	130	19.3	65.9	14.8
1944/45	295	8.8	67.6	23.6
1948/49	327	29.0	63.0	8.0
1949/50	711	29.5	64.7	5.8
1950/51	901	11.3	76.9	11.8

¹²At the International fur auction in Leningrad in 1961 the most expensive skin 511 of the extremely valuable Barguzin sable was sold for four hundred and five dollars, and the very cheapest of the same race, for twenty dollars (B.A. Kuznetsov)—a ratio of 1:20. It is natural that, in evaluation, all the characteristics of the skin played a signal role (fluffiness, softness, delicacy, luster of the fur, grizzling, size etc.). However, color is one of the main characteristics.

Similar to this type of change in fur color of various races and populations, there are, apparently, also changes which take place in one direction for a quite extended periods. Thus, in regions of Siberia adjacent to the Yenisei beginning at the end of the 1940's the color of the sables gradually started to lighten, and still continues at the start of the sixties. Even the release of dark Barguzin sables in some regions did not prevent this process (Tashtinsk, Yeniseisk and Turukhansk regions, 1949–1957). In some parts of the range, a darkening of color in the population is observed (K.D. Numerov).

There may occur in skins an admixture of pure white guard hairs, giving the beautiful "grizzled" fur. This admixture may be great ("grizzled sable") or negligible, or completely absent ("glukhaya sable"). White sables (albinos), chromistic and skewbald (with white spots) may be found as exotypic variations. Sables with a bright orange tint as well as gray may also be encountered.

Sexual and age difference in the color of sables is absent. Young sables in their first autumn are clad in adult coats.

The skull of sable is relatively narrow and elongated. Both the facial and particularly the braincase are elongated. The distance from a median line joining the ends of the postorbital processes to the alveoli of the middle incisors constitutes more than 65% (but less than 80%) of the distance from the same line to the posterior point of the occipital crest. The muzzle is relatively narrow. Nasal bones have usually fairly sharp constrictions in their middle portion. Zygomatic arches are relatively thin, the supraorbital processes are well developed and broad, and the postorbital constriction is wide (more than the width of the skull above the canines).

The mastoid processes do not protrude beyond the lower margin of the auditory meatus. The sagittal crest is only developed on the posterior-most part of the cranium and the occipital crest is weakly developed. Bones of the auditory bullae are relatively swollen in a longitudinal direction and close to each other: the distance between them in their median point of their length is less (rarely equal to) than half the distance from the anterior end of the chamber to the posterior edge of the paroccipital process. The auditory tubes are well developed.

The longitudinal diameter of the upper carnassial tooth is approximately equal to the transverse diameter of the upper molar. In this latter the inner blade is considerably larger than the outer.

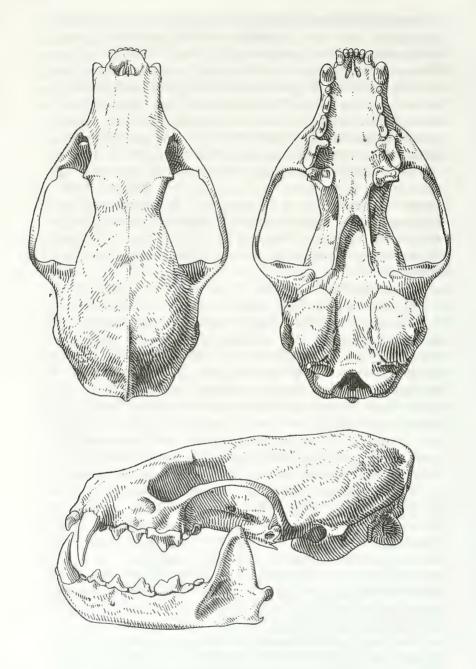


Fig. 191. Skull of the sable, Martes (Martes) zibellina L.

Sexual differences in the skull are insignificant and represented only in the somewhat smaller dimensions of the female skull. Age variation is quite great. Besides the increase in general dimensions, with age the skull acquires a more elongated form, and the zygomatic width increases as does interorbital width. On the other hand, the postorbital constriction of the skull (behind the supraorbital processes), narrows. The interorbital width in males 8–9 months old constitutes 18.5 mm on the average, while an animal older than 3 years is 20.2, corresponding postorbital constriction is 18.0 and 15.5 mm. With age the so-called "temporal lines" which outline the region of attachment of the masseteric musculature to the braincase, gradually approach each other, and the sagittal crest is formed on the skull by the time of sexual development of the animal.

According to the character of these lines and other characters, the following age groups of sable are distinguished (Fig. 192; Nadeev and Timofeev, 1955).

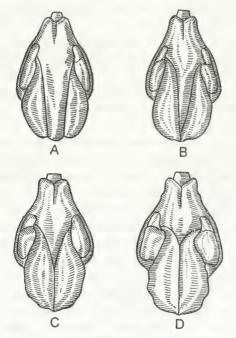


Fig. 192. Schematic outlines of sable skulls of different ages. From Nadeev and Timofeev, 1955. A) Age group I—8-10 months; B) Age group II—1 year, 8-10 months; C) Age group III—2 years, 8-10 months; D) Age group IV—about 3 years, 8-10 months and older.

Age I—young animals 8 to 10 months old, *i.e.* middle of first winter of life. The temporal lines separated and extend parallel to each other, only sometimes approaching each other at occipital crest, but do not fuse. Form of skull is rounded. Occipital crest is rarely visible, and the sagittal is absent. Incisors not worn, or very slightly obliterated. Ratio of interorbital width to postorbital in males, 0.84–1.17 (M 1.06); in females, 0.78–1.14 (M 1.06).

Age II—about 1 year, 8–10 months old (middle of second winter of life). Occipital crest well developed. There is a rudimentary sagittal crest, temporal lines come together posteriorly forming an acute angle. Incisors slightly worn. Ratio of interorbital width to postorbital in males, 1.04–1.22 (M 1.10); in females, 1.04–1.24 (M 1.11).

Age III—about 2 years, 8–10 months old (middle of third winter of life). Occipital crest is moderately or strongly developed. Temporal lines come together in blunt angle at anterior half of braincase, in posterior part form well-developed sagittal crest. Ratio of interorbital width to postorbital in males, 1.09–1.37 (M 1.20); in females, 1.08–1.33 (M 1.17).

Age IV—about 3 years, 8–10 months old (fourth winter of life and older). Occipital crest strongly developed, sagittal crest is moderately or strongly developed—it extends along the entire braincase; temporal lines absent (evident only in interorbital region). Ratio of interorbital width to postorbital in males, 1.14–1.55 (M 1.30); in females, 1.17–1.43 (M 1.24).

The majority of the above-mentioned features, and above all, the position of the "temporal lines" and the development of crests, are determined by increase in mass of masticatory musculature with aging, and by their growth upward from both sides to meet each other. If in the young animal (Age II) this musculature is relatively small and muscles of the right and left sides are separated, then by Age III, they are closely appressed along the sagittal plane and lie on the braincase as a solid elongated mound (Fig. 193).

The tail skeleton consists of 15–18 vertebrae. The os penis is forked at its distal end, and the ends of this fork may be directed toward each other, forming a half-ring, but they do not close the ring. The length of the ossicle in Trans-Ural sables is 39.2-M 41.4–43.2 mm (Yurgenson 1947)¹³. Intestine length is 1000-M

¹³Other features in the structure of this bone given by Ognev (1931) and used by Novikov (1956) are not constant and not characteristic.

515

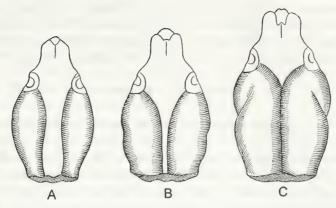


Fig. 193. Position of masticatary musculature in different age groups of sable. Groups [A, B, C] are those given on in previous figure [Fig. 192] from Nadeev and Timofeev, 1955.

1790–2700 cm, which constitutes 250.0–M448–630.0% of the length of the carcass without the hide (365–M422–490 mm). Heart weight is 5.23–M8.82–15.20 gm, or 9.0–M12.2–21.5‰ (n 117); lung weight (without trachea) 8.10–M14.9–52.50 gm; liver weight 10.32–M14.90–45.7 gm; kidney weight 1.40–M2.76–5.35 gm; spleen weight 0.62–M1.65–3.90 gm 14 (Timofeev and Nadeev, 1955). The diploid number of chromosomes—38 (V.N. Orlov).

Dimensions (extreme variants for the species) of sable are as follows: length of body of males, 375-580 mm; of females, 320-510 mm; tail length of males, 110-170 mm; of females, 90-176 mm; hind foot length of males, 70-105; of females, 60-90 mm; ear length of males, 50-56, of females, 43-55 mm.

Condylobasal length of skull of males, 74.1–94.6 mm; of females, 70.0–84.4 mm; zygomatic width of males, 38.7–56.2 mm; of females, 32.9–52.8 mm; skull height of males (together with auditory bullae), 27.0–37.4 mm; of females, 26.5–39.6 mm (after material of Nadeev and Timofeev, 1955).

Weight [in gm] of males (22) of Yenisei sables in January, 1110-M1472-1810, of females (21), 820-M1132-1560. Weight in July in males, 1200-M1433-1810; in females, 870-M980-1300 (Kuznetsov, 1941). Optimal weight of breeding sables before the

¹⁴The relative weight of all organs is overestimated, since it was determined according to the weight of the carcass without the hide. Its [hide] weight (n 230) is 440–1300 gm (M 730.5).

beginning of rut (15 July) in captivity (Pushkin fur farm): males with body length between 39 and 49 cm, 1400–1900 gm; females with body length between 36 and 46 cm, 900–1400 gm (Starkov, 1947). The maximum known weight of a male is 1869 gm (V.H.).

Systematic Position

The sable is a typical representative of the genus *Martes*, closely related to the true martens; as with all of them, it is quite sharply distinguished from the fisher, *M. pennanti*. At the same time, the characters of the forms *zibellina*, *martes*, *foina* and *americana* are combined in individual species in quite complex assortments which do not permit arranging them in a successional series. However, it is evident that of our two martens, the pine marten (*M. martes*) is more closely related to the sable. This is indicated not only by a series of similar features in their morphological characteristics, but also by the hybridization of these species in nature ("kidas"¹⁵), and by the fertility of the hybrids in the back-crossing. Notwithstanding all of that, obviously the species independence of sable and marten are accepted in what follows.

It is possible that the American marten *M. americana* belongs to the species *zibellina*, although it has several marten features (bones of the auditary bullae). In any event, the sable, pine marten and American sable themselves represent a close group. It is quite possible that the sable should be considered the less specialized form of this group and thus (perhaps together with the American sable) the least specialized species of the genus (V.H.).

Geographic Distribution

Forest regions of Siberia, northern Europe, Mongolian Republic, northeastern China, the Korean Peninsula and Japan.

Geographic Range in the Soviet Union

This constitutes the overwhelming part of its range. It occupies a great part of the state territory—all the forested part of Siberia and the northern European part of the USSR.

516

¹⁵For details about kidas, see the section on pine marten.

Determination of the natural range of sable presents great difficulties. In the European part of the USSR the sable was subjected to intensive pursuit over the past thousand years, and in Siberia, over the past few hundred years. By the twentieth century not only had the number of sable decreased a hundred-fold, but also the general extent of its range was very sharply reduced.

The sable is associated with forests, first of all with taiga; however, it is ecologically quite flexible and within the forest zones it is met with under entirely different conditions-from thickets of prostrate nut-pines in the high mountains to low land swampy taiga, and from forests of the Amur type to forest-steppe islands and riparian forests. This allows one to think that, in the past, the sable occupied the entire forest zone of Siberia. There are indications of its occurrence in the forest-tundra, at least the southern extreme, not only in the past, but also at the present time.

One may consider that the natural range of the sable was continuous. There were, of course, more or less significant openings and gaps in it, related to natural landscape conditions (for example, Minusinsk steppe). However, they themselves constituted exceptions, and their area was immeasurably smaller than regions inhabited by the sable.

Reduction in the range of the sable was quite unique and took place in two ways. On one hand, mainly in the south, but also in the west and the northeast there was recession of the limits of the range. On the other hand, within the boundaries of the range, great expanses were formed in which the sable has completely disappeared. Thus, the range was broken into separate parts. This was the chief way the range was reduced—the general areal extent of the sable's disappearance is no larger an area than that in which it persists.

The separate areas inhabited by the sable became transformed into "islands", usually small, and in the majority of cases, especially in the east, they are so completely isolated from each other that their natural restoration, given the cost of restocking, seemed 517 impossible. Along with their direct pursuit and destruction, a large, although not so significant, role in the reduction and fragmentation of the sable is range was played by the felling, burning and ploughing up of the taiga, which was gradually taking place on a large scale, and in particular forest fires.

The picture of the range described at the beginning of the 20th century, was the result only of destructive human activity. As indicated by experiences in our day, the sable is quite viable and completely "contemporary" and, by no means, is going to become extinct, as some have attempted to portray it.

The destruction of sable started so long ago, that, with the scarcity of historical data—above all, about Siberia—to restore the picture of its range is now quite difficult. Proceeding from the ecological characteristics of the sable, in regard to some territories one may consider that the actual range in those places was greater than that drawn on the basis of contemporary data and historical information. It is particularly difficult to establish a picture of the range of the sable in the European part of the USSR. The views presented by different investigators about the previous limits of sable distribution in this part of the country are entirely at variance.

After reaching its minimum and extreme of fragmentation at the beginning of the first decade of the 20th century, the range increased somewhat by the beginning of the second decade, during the period from 1912 on of complete prohibition of its hunting and in connection with other circumstances. By the third decade, it was again reduced. By the end of the 30's and in the 40's and 50's, not only did the number of sable increase by several times, but its range area had strongly extended as a result of legal protection, conservation and reintroductions. Protected areas inhabited by sable have increased, uniting several previously isolated areas again, and new sables appeared in those places where they had been long absent. In this way, in the last ten years the sable's range was found to have changed rapidly. This also makes the definition of distributional data quite difficult.

The history of the range of the sable is a clear example of a range change occurring under the influence of the anthropic factor—at first, its deep, uncontrolled destruction, and then its planned restoration. Naturally, the range of sable cannot be fully restored to its previous size, because in some places natural conditions have been so intensively changed that they became unsuitable for the existence of the species. However, at the present time, not all possibilities have been employed to restore the previous range of the sable.

The outlines of the westernmost part of the range in the past (historical time) cannot now be reliably and completely restored. If there is more or less reliable information, not disputing the existence of disagreements, along the Urals and the northeastern European part of the Union, westward to Severnaya Dvina then the question of the occurrence of sable farther to the west is not so clear. Its discussion dates back almost one hundred years; nevertheless, in quite distant times as well as more recent years, very competent authors (Middendorf, 1867; Sabaneev, 1875; Zhitkov 1937), regarded information on the occurrence of sable in the European north, northwest and west with great scepticism or denial. In recent years, however, new materials have been found (Kirikov, 1952, 1958, 1960) which reopened anew the discussion of this question¹⁶.

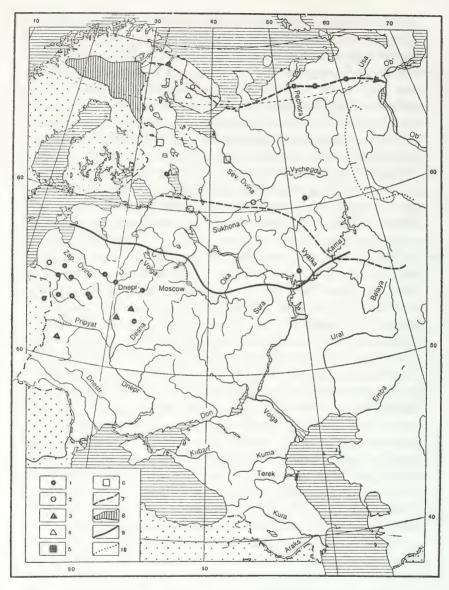
The localities farthest west for which there is mention of the

519

presence of sable are located in Lithuania. Byelorussia and Smolensk oblast. Besides Lithuania in general, the sable was also noted in Vil'nyus and Kaunas, Zelenaya Forest in the former Ponevezhsk county and near Knyshin city (now in Poland to the northwest of Belostok—the westernmost point; in the 16th and the first half of the 17th century). In Byelorussia, Minsk, Lutsk (now Volynsk district in the Ukraine; the southernmost point, about 51° N. lat.), Novogrudok (Middendorf, 1867), Polotsk, Vitebsk, and Grodno were mentioned as places inhabited by sable in the 18th century; in the 1880's, sable was noted in Belitsk and Klimovich counties; in the latter, at the border with Roslavl' county of Smolensk governance. There is mention of the occurrence of sable around Smolensk at the beginning of the 17th century, and in 1668, in Bryansk forest, which was contiguous to the south with Byelorussia. Therefore, old data on sable occurrence in Lithuania and Byelorussia are substantively reinforced.

In the north, to the west of the Northern Dvina, sable were noted within the limits of our country on the Sun' river, which

¹⁶Here data on the occurrence of sable in the west are laid out very briefly and schematically, chiefly after Kirikov, 1952, 1958, 1960, as well as Middendorf, 1867, Polyakov, 1873, Sabaneev, 1875; Pleske, 1887; Ognev, 1931; Yurgenson, 1933, Zhitkov, 1937; Van den Brink, 1958 and several other sources. Separate references are only given in the case of their absence in S.V. Kirikov. It must be taken into consideration that the data of Sabaneev (1875) on westward transgressions of sable, which are commonly used (Ognev, 1931 and others) are taken from Middendorf (1867) and contain little that is original.



518 Fig. 194. Data on the past and present distribution of the sable, Martes (Martes) zibellina L. in Europe. V.G. Heptner: 1—concrete, and 2—generalized mentions of the occurrence of sable during the 16th and 17th centuries; 3—concrete, and 4—generalized information for the 18th century; 5—concrete, and 6—generalized information for the 19th century; 7—probable northern and southern limits of the range in the northern European part of the country in the past; 8—limits in the (contd.)

flows into Onezhsk [Onega] lake from the northwest (middle of the 17th century)¹⁷, in Lapland (in the 17th and 18th centuries), and particularly on the Kola [Peninsula] at the end of the 17th century, where in 1834 it was still found somewhere in the northern parts of present Karelia (Kemsk county of Arkhangel'sk governance), and in the former Kholmogorsk county, and in the 16th century, in Velikii Ustyug district. This is the southernmost place of occurrence of sable in the section of the northern European part of the USSR under consideration.

Concerning Finmark, the sable is mentioned in Scandinavian folklore in the 9th–10th centuries. Finally, northern Finland and northern Sweden hosted the occurrence of sable in the past (about 300 years ago). Here, the range forms an irregular triangle lying at the eastern border of Finland, approximately between 65° N. lat. and Lake Inari; its apex is located somewhere a little south of Kirun in Sweden (Van den Brink, 1958).

The materials given above show that the range of the sable in the west occupied the taiga of Arkhangel'sk district, Kareliya, and the Kola Peninsula, and extended to Finland and Sweden.

Concerning the districts lying to the east of the Dvina and Ural [rivers], the Cis-Urals and the Urals [mts.] themselves, there is a body of sufficiently accurate information indicating a considerably wider distribution of sable in the past. In the 16th–17th centuries, the sable was, apparently, widely distributed along the Mezen' and its western tributary, the Vashka (Udor), *i.e.* evidently also in the interfluve between it and Dvina. Concerning the Mezen' and Vashka, there is also information up to the middle of the 19th century. In the north, sable extended to Pustozersk in the lowermost Pechora, and approximately along this latitude the northern border of its range reached to the mouth of the Ob' river.

In the Vychegda basin, sable existed and were still quite common at the beginning of the 17th century, being found not only

(Fig. 194 contd.)

extreme northwest in the past (Van den Brink, 1958); 9—probable southern limit of the range in the Neolithic (Yurgenson, 1933 with modifications); 10—recent (in 1960) western limit of sable range. In Byelorussia and Lithuania, in Kareliya and on Kola Peninsula, all data points in literature are presented, in remaining sections—only individual peripheral points.

¹⁷In the manuscript of the monk Epifanii—a minor companion of Protopop Avvakum whose personal report of the place is ascribed to one hunter, who said: "would it be any wonder, if ... God sent precious sable or fox or other animals ... all animals and birds to live here" (report of A.N. Robinson).

along the right (Yarenga, Vym' and others), but also along its left (southern) tributaries—the Sysola as well as Bolshaya and Malaya Vizinna*, Lop'yu and others (Kirikov, 1958, 1960). Even in the 19th century, sable lived in the Vishera basin, in the neighborhood of Cherdyn' and in Cherdyn' county, along the Chusovaya, and in earlier times, they lived at these latitudes even farther to the west.

Sable also occupied the western parts of present Komi ASSR and all of former Permsk governance, *i.e.*, the territory to the east of 54° E. long., which nearly corresponds to present Permsk district (Sabaneev, 1875). Approximately to this line or a little to the west, there are mentions referring to Biserovo at the sources of the Kama to the northeast of Omutninsk, on the Ponino* a little north of Glazov, at the sources of the Vyatka and in the region of Sarapul (Shaberdin and Strel'tsov, 1930; Yurgenson, 1933). The supposition concerning the occurrence of sable in the eastern half of the former Vyatsk governance (Sabaneev, 1875) is supported by documented places of occurrence; however, concerning more western regions, *i.e.* to the west of approximately the 47–48 meridian [E. long.], concrete data are absent. (Data of Shaberdin and Strel'tsov are, however, not very definitive, since they report the capture of kiduses even in 1928/29).

Farther to the east, the border was deflected, turning south and proceeded into Krasnoufimsk, embracing the forests along the Tyusha, B[olshaya] and M[alenkaya] Sarsa, B[olshaya] Sarana and Kashanka [rivers]. Still further south, there is evidence on the occurrence of sable in the 18th century in the Urals in the upper Ufa river (Pallas, 1786) and along the southwestern slope of the Urals to the east of the city of Ufa even in the first half of the 19th century (Sabaneev, 1875)¹⁸.

The true southern border of sable distribution in the Urals in the time under review, has apparently, extended somewhere in the

^{*}Not found-Sci. Ed.

¹⁸References sometimes occur in literature on the occurrence of sable in the past near the city of Ufa. This is the result of secondhand rewritings and simplification of original sources. Pallas (1786) writes: "It sometime happens, though quite rarely, that along the Ural mountains, and especially in Kama, and along the upper Ufa river outliers of sable appear (page 25; information dated from 1770). Sabaneev (1875, page 201) reported that the last sable, killed "on the southwestern slope of the Urals", was near Berezovka village, Ufimsk county.

region of 55–56° N. lat.—the sources and upper reaches of the Ufa (Pallas, 1786) and Kaslinsk mountain (Sabaneev, 1875)¹⁹.

In summarizing everything said, it is possible to accept that, in historical time, and, still in part at the end of the 18th and even the 19th centuries, the southern boundary of the range of sable in the European part of the USSR began in the Urals at about 55–56° N. lat., crossed the Ufa in its upper or middle course, extended to the Kama somewhat above the mouth of the Belaya, passed thither to the upper Vyatka and farther to the region of Velikii Ustyug. Thence, it turned directly westwards to Olonetsk territory (southern Kareliya), passing somewhere through the region of Lake Onezhsk [Onega], possibly through its middle, or even southern, part²⁰.

Beyond this line, it is possible that separate areas of occurrence were found in Lithuania and Byelorussia. It is worth noting, however, the complete absence of information from Moscow, Ryazan and other middle-Russian regions, about which there are many historical documents, and in general, about the whole extensive area between Lithuania and Byelorussia, on one hand, and Arkhangel'sk and the Olonetsk forest, on the other. It is possible that in previous centuries, a separate focus of sable inhabitation, isolated (artificially?) from the main range was found in the southwest, similar to several of the present Siberian outliers. The reality is that it lies to the south of the southern border of Neolithic sable fossil finds as they are known to us at the present time (see below).

The northern border of the range extended, apparently, along the northern border of the forest—in the west, Kola was mentioned and in the east—Pustozersk, and along the border of the forest lying to its east, *i.e.* north of the Arctic circle. In the Urals, the northernmost point inhabited by sable was, apparently, the Voikor river—an Ob' tributary at its mouth on the Arctic circle²¹.

¹⁹Sabaneev's assumption (1875, page 200) that it extended to 52° "perhaps 51° N. lat.", is not based on factual material. Rychkov (1762) directly affirms that "sable occurs nowhere in Orenburg province (which at that time included the South Ural; V.H.)." To postulate the existence of sable south of 55–56°, is now only possible by analogy to some other northern species which descend along the Urals south as far as 52°, and for very remote times. Evidence concerning 51°, accepted by many authors after Sabaneev, is based on misunderstanding,—this parallel passes south of the Ural river along the steppe.

²⁰There are data on the occurrence of sable around Arsk northeast of Kazan in the 16th century (the manuscript of Prince Kurbskii; after Kirikov, 1960), but this point remains strongly isolated spatially at present.

²¹All places, especially where no reference was cited, are taken from S.V. Kirikov (1952, 1958, 1960). The boundaries herein, however, have a different outline than in the map of S.V. Kirikov (1960).

Urals.

The interpretation suggested here of the previous range of sable in Europe agrees well with the limits of the range in the Neolithic, which generally corresponds to the outline of the [present] southern limit of the sable's range, but considerably more to the south. This line (Yurgenson, 1933 with modifications) passes from the northern part of the Gulf of Riga across the lower Velikaya river, above Pskov, proceeds a little south of Lake Il'men' and somewhat more to the north of Seliger and extends through the Kimp region. Thence, it descends to the southeast, embracing Meshchera, proceeds somewhat more to the north of Kasimov, crosses the Oka [river] above Murom, the Sura in its lower reaches and the Volga

The substantive point in the line described is that it passes, in the west, approximately intermediate to the described northern points of possible habitation in the Lithuanian-Byelorussian region and the southern limit of the region of previous inhabitation in the area between the Urals and Scandinavia.

slightly above the mouth of the Kama. This recent boundary crosses the Vatka at about 50° E. long.—in its lower reaches and again crossing the Kama above the mouth of the Belaya, reaches the

Evaluating the previous range of sable in North Europe, it must be emphasized that it is, in a zoogeographical sense, regular. Some Siberian taiga species analogous to sable, such as northern red-backed and gray red-backed voles (Clethrionomys rutilus, C. rufocanus), wood lemming (Myopus schisticolor) and in part Siberian chipmunk (Tamias sibiricus) extend very far to the west in the north of our country—all, except the chipmunk, to Scandinavia. However, the presumption of sable occurrence in Lithuania and Byelorussia is not predicated on this type of range.

All the mentioned materials, even if the evidence concerning Lithuania and Byelorussia is disregarded, demonstrate the fault in the view of both old and new authors that the sable was not distributed far to the west in the past²².

The present (50's) western limit of the range of sable takes the following form. In the north, it begins slightly to the north of the

²²Middendorf (1867) affirmed that sable never existed to the west of Syktyvkar (Ust'-Sysol'sk). Nadeev and Timofeev (1955) believed that "in Europe, sable ... in the past penetrated a very small distance". Zhitkov (1937), Poluzadov (1955) and others held the same view. Sabaneev (1875) did not exclude the possibility of far penetration of sable to the west, but doubted it and only Pleske (1886) believed in the existence of sable on the Kola Peninsula still in the 18th century.

sources of the Lyapin at approximately the latitude 63° 30′ N. lat. (a little south of the limit of nut-pine) and passes south along the western slope of the Urals through the upper Shchugor, Ilych, Pechora (including the Pechoro-Ilych preserve), Un'va and to the sources of the Yaiva. Thence, the range boundary turns sharply to the east, passing through the basin of the Kakva river a little north of the city of Serov, crosses the lower Loz'va and continues to the Tayda and farther, towards the upper Noska river which flows into the Irtysh below Tobol'sk. It is possible that boundary line extends (or not long ago) to include the region to the west where the Usa flows into the Pechora, and southward, the Troitsk-Pechorsk region (V.Ya. Parovshchikov). To the north of the sources of the Lyapin, it passed to the southeast in the general direction of Berezovo on the lower Ob' (Shvarts, Pavlinin and Danilova, 1951; Nadeev and Timofeev, 1955; for more detailed delineation of the Ural center of sable occurrence, see Fig. 198).

The northern border of the range in Siberia begins in the Urals, on the Voikar river near the Arctic Circle and passes eastward across the lowest reaches of the Ob', apparently, approximately along the tree-line, *i.e.* somewhat south of the southern shore of Obsk Bay. In any case, this line included the basin of the right tributary of the lower Ob', the Kunovat river (65° N. lat.). Along the Taz, the range extends to the Arctic Circle and, perhaps, a little across it (V.N. Skalon). From the Taz, the border passes to the northeast, including the basins of the B[olshaya] and M[alaya] Kheta (left tributaries of the Yenisei); crosses the Yenisei somewhere in the Dudinka region and rises along the right bank of the Yenisei to the region of Lake Kit (of the Noril'sk group) and upper Noril'sk creek. It falls only slightly short of Noril'sk and here attains a latitude of 68° 40′ N. (Podarevskii, 1935) or even includes Lake Pyasino and the upper Pyasina at 70° 30′ N. (Kirikov, 1960).

Further, the sable is known at Volochanka on the Kheta, *i.e.* approximately around 70° 50′ (Orlov, 1930). To the east, on the Khatanga, the border goes, apparently, to about 70° or slightly more to the north, crosses the Khatanga approximately at a latitude 69° 30′ (Nadeev and Timofeev, 1955) or more to the north (Staraya; A. Romanov, 1941). It reaches the Anabar, approximately at a latitude of 70° 50′, on the Olenek—at 69° 30′, the Lena at the same latitude or at 69° (finds are known at Zheldong 250 km below Zhigansk; Tugarinov, Ivanov and Smirnov, 1934) and on the Omoloi.

The range boundary crosses the Yana somewhere below Verkhoyansk, probably about 68°, includes the basins of the Chondon and Khroma (Kirikov, 1960) crosses the Indigirka about 69° or a bit southward (D. Ivanov) and reaches the Kolyma below Sredne-Kolymsk. On the right bank of the Kolyma, the range encompasses not only the Omoloi basin, but also the Bol'shoi and Malyi Anyui (Middendorf, 1867). From the Anyui, the range border crosses the Anadyr' covering, apparently, its upper and middle course, and across the Khatyrka and Opuka basins, reaches the coast of the Bering Sea in the region of the mouth of the Opuka, a little to the south of Cape Navarin (Samorodov, 1939; Portenko, 1941).

The description given of the northern border of sable range in Siberia was constructed on the basis of direct evidence of its contemporary distribution and its distribution in relatively recent past. It is, however, well founded (archival material dated from the 16th century; Kirikov, 1958, 1960), that in the expanse from the Ob' to the Kolyma, the actual natural range boundary ("reconstructed") coincided with the northern forest limit (see map). Therefore, between the Ob' and the Yenisei, it lay a little to the north, and between the Yenisei and the Kolyma, significantly more to the north than as shown. The described section of the border east of the Kolyma corresponds to the reconstructed [border]. In some places on the northern border, the sable also lives outside the [taiga] forest zone—in krumholz, in deciduous forests of river valleys (Anadyr') and in nut-pine thickets (Koryatsk land).

The shore of the Pacific Ocean constitutes the eastern range boundary. Within the range are Shantar and Sakhalin islands. Of the Kuril islands, the sable is shown to have resided on Iturup and Kunashir (Snou, 1902; Voronov, 1963), and to the north, on Paramushir (Kuznetsov, 1949). The latter was shown, evidently, to be mistaken (Voronov, 1963), on Karaginsk Island, the sable is absent, as on the Commanders.

The southern border of the reconstructed sable range began in the Urals in the upper Ufa at a latitude 55°-56° (see above) and entered Siberia near Chelyabinsk (Pallas, 1786). Further to the east, the border passed through the whole of eastern Siberia in the forest-steppe zone. From Chelyabinsk, it went along the so-called "Isetsk province", apparently through Kurgan [city], or between it and Yalutorovsk, and farther to the city of Ishim or south of it and

reached the Barabinsk forest-steppe. Here the range boundary went to the mouth of the Om, apparently, north of Lake Chana and reached Lake Ubinskoe and to the Ob' at Novosibirsk. This is the border in the 17th century, and, in some places, the 18th century (Pallas, 1786; Sabaneev, 1875; Ognev, 1931; Kirikov, 1960).

From Novosibirsk, the boundary turned sharply to the south and passed towards the foothills of Altai, apparently in the Biisk region. Here, the border turned back to the west and then to the south and southeast, embracing the Altai. In this region, the boundary again passed along the edge of the foothill forests at the latitude of Bijsk; farther, it passed around the Tigeretsk range to the north, continuing somewhat to the east of Zmeinogorsk, and then from the western end of the range, along the Uba, Bukhtarma and Ul'ba basins, almost reaching the Irtysh. In the south, the bound-524 ary included the Kurchum and the region of Lake Markakol' (Ognov, 1931; Yanushevich and Blagoveshchenskii, 1952; Afanas'ev et. al., 1953; V.G. Heptner). At Markakol', the boundary of the range reached the state border²³. It is probable that the Altai portion of the sable range was somewhat broader. It may be that sable lived also in the ribbons of forest in the Cis-Altai steppes and extended south to the Irtysh. However, there is no information on this point.

In the expanse from the southern Altai to the Pacific Ocean, the sable range reaches the state border (Tannu-Ola, for instance) or beyond it. In Ussuri Territory, the sable is known as far south as the Kedrovaya river (Kedrovaya Pad' preserve) between Vladivostok and Pos'et (Ognev, 1931), *i.e.* almost to the state boundary. The range does not include the steppes of southeastern Trans-Baikaliya, the steppe areas along the Onon northward to the lower Ingoda and upper Shilka and eastward approximately to 52° N. lat. in the north.

The reconstructed range outlined above for sable, apparently was never completely continuous, but apparently, significant gaps were not present in it because of the great ecological flexibility of sable. However, long ago—in some places in the 16th century and

²³According to Sabeneev (1875, map), the range included a considerable part of the left bank of the upper Irtysh and across the Alakol'sk lakes (!) it extends to Issyk-Kul'. These rough misrepresentations were based on the extremely confusing and completely false view of N.A. Severtsov (1873) about the fact that in Tien Shan, three marten species existed—the pine, stone martens and the sable ("Kashgarsk sable"); however, in this region, they were not yet fully differentiated. The echos of these views persisted in literature almost to the present time.

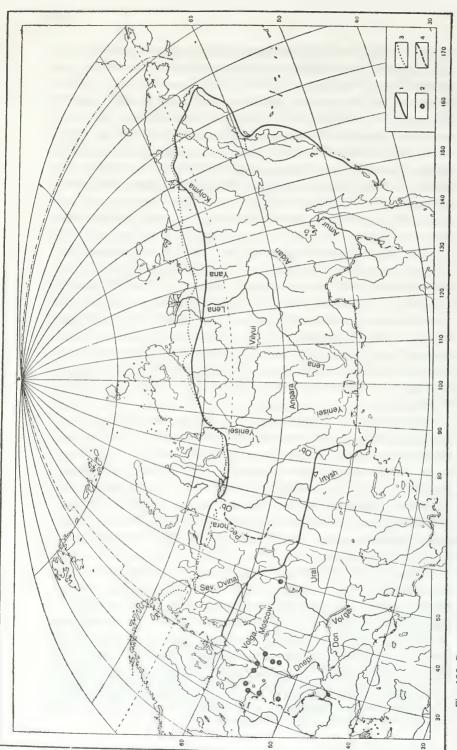


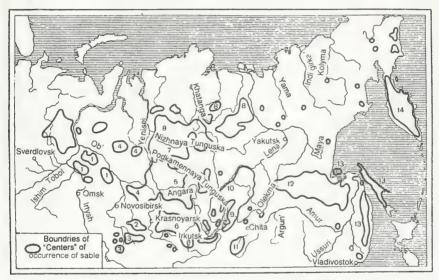
Fig. 195. Reconstructed range of the sable Martes (Martes) zibellina L. in the USSR. V.G. Heptner: 1. Range boundary; 2. Peripheral points the mouth of the Pechora the northern border of sable distribution apparently coincided with the forest border; 4-Recent (1960) western border for which occurrences of sable are known in Lithuania and Byelorussia in the past; eastern point—Arsk; 3—Northern limit of forest. West of

of sable distribution.

very clearly in the 17th century—the sable entirely disappeared in considerable areas both at the periphery of the range (west Siberian forest-steppe and other places) and also within it.

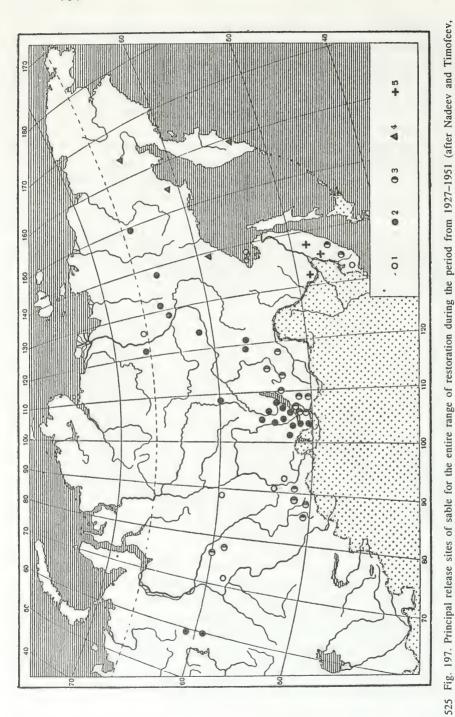
By the 20th century, this process attained its culmination and the sable range displayed a fragmentation into few more or less considerable sections and a large number of very small ones. All of them were isolated from each other.

At the present time, despite the very great restoration of the range, as compared to the beginning of the current century, it still remains fragmented into separate parts, some massive and some relatively small. The regions inhabited by sable are as follows (Fig. 196).

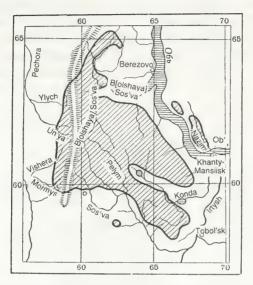


524 Fig. 196. General scheme of recent range of the sable in the USSR. Figures designate the separate "centers" of occurrence. Data up to 1950 (after Nadeev and Timofeev, 1955, simplified).

To the largest regions belong: Ural-Ob', occupying the Urals and left bank of the Ob' (Fig. 198); Yenisei, lying along right bank of the Yenisei northward approximately from 57° N. lat.; Sayan, occupying Sayan and Tuva; Lena—between the Lena and Vilyui; Vitim-Trans-Baikaliya lying along the upper Lena, Vitim and along the eastern shore of Baikal; Aldan-Zeisk, situated between the Aldan and lower Amur; Kamchatka, occupying the entire peninsula. There are many smaller regions of less practical importance: Sakhalin,



1. Sites where native form was released, 2. Sites where Vitim sable was released into region of occurrence of another form, 3. Same for Buryat sable, 4. Same for Kachatka sable, 5. Same for Bureinsk sable 1955, with modifications).



526 Fig. 198. Boundary of sable distribution in the extreme west of the range—in the Ural-Ob' region of occurrence (after Nadeev and Timofeev, 1955).

Ussuri, southern Trans-Baikaliya and Altai. Between these centers are interspersed, still smaller and sometimes very small regions of sable occupation, sometimes lying very far from each other, as in Yakutiya (after Nadeev and Timofeev, 1955; the names of the separate centers do not correspond to those given by these authors).

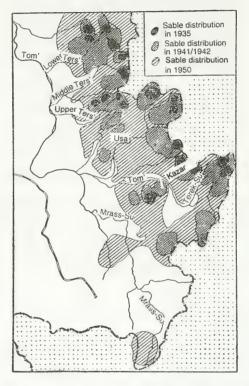
Geographic Range outside the Soviet Union

The (re-established) range includes the northern part of the Mongolian Republic, northeast China, the Korean Peninsula and Japan.* In the Mongolian Republic, the re-established range occupies Mongolian Altai (sources of Chernyi Irtysh, region southwest of Kobdo) in the southeast to the Bulgun river (about 92° E. long.), the region west and east from [Lake] Kosogol, Khangaisk montane country south to the upper Orkhon, and westwards including Selenga and Egin-Gol regions. Apparently, an isolated area of occurrence is found in Kentei south to Bogdo-Ula (a little south of Ulan-Bator), and eastward including the upper Onon and Kerulen. The existence of sable was also recorded in the Mongolian part of the

^{*}Hokkaido only-Sci. Ed.

Bol'shoi Khingan [range]. At the present time, sable exists only in Mongolian Altai, Pri-Kosogol'e and Kentei, except for the Onon and Kerulen. It is absent in the Khingans (Bannikov, 1954).

A finger of the range which extends south along the Mongolian Altai, apparently transgresses somewhat into Chinese territory.



526 Fig. 199. The course of the natural increase in sable range in the center of occurrence associated within Kuznetsk Altai (upper part of Ob' basin) (after Nadeev and Timofeev, 1955, somewhat simplified).

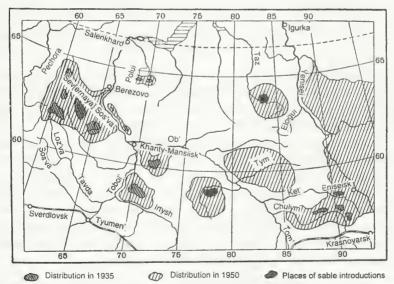
In northeast China, the natural range of sable occupies almost all the country except the Barga steppe and the plains of the former Central Manchuria. It exists in the Bol'shoi Khingan, Il'khuri-Alin and Malyi Khingan which extend into the northern part of the country along the Amur, in the mountainous country east of the former Manchuria—between the central plains and the Ussuri and

528 in the mountains bordering the Korean Peninsula (Chanbaishan' mountains). At the present time the sable population is strongly depleted, and exists chiefly along the Bol'shoi Khingan and in the northeastern part of the country (Baikov, 1915; Sowerby, 1923; Lukashkin and Zhernakov, 1934 and others). Details of sable distribution on the Korean Peninsula are not known. In Japan, its geographical distribution area includes Hokkaido Island, Honshu (Hondo), Shikoku, Kyushu and Tsushima* (V.H.).

Geographic Variation

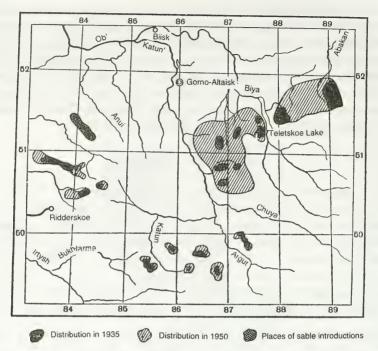
Geographic variation in sable is well marked, and if taken in the sense of morphologically extreme forms, the amplitude of variation is quite significant. This variation is expressed in general body and skull dimensions (its proportions are nearly invariable) and, particularly, colors. Fur quality varies considerably: its density, fluffiness, softness and fineness.

Geographic variations in sable have been noticed and employed practically in the fur trade for a long time, where they were



527 Fig. 200. Growth of sable range in the Ob'-Yenisei section of the range (in part with introductions) (after Nadeev and Timofeev, 1955, simplified).

^{*}Populations south of Hokkaido are now usually considered a distinct species, Martes melampus—Sci. Ed.



527 Fig. 201. Dispersion of sable and increase in its range in Altai (after Nadeev and Timofeev, 1955, somewhat simplified).

529 eloborated into a detailed and in its main features orderly and natural system of sable fur "grades". It found its expression in difference in prices of sables from different places, differences that were already established a very long time ago²⁴.

Serious study of geographic variation in sable from the zoological point of view began only in the 20's of this century (Ognev, 1925, 1931), although individual reports appeared earlier (Birulya, 1916, 1918) and attempts at analysis were made more than 100 years ago (Brandt, 1855). The latest scheme of variation in the species over its entire range in the USSR, based on significant material was carried out only in the last decade (Kuznetsov, 1941; Nadeev and Timofeev, 1955).

²⁴At the International fur auction in Leningrad in 1961, the highest lot price of sables of various grades was as follows: Tobol'sk—28 dollars, Altai—30 dollars, Amur—31 dollars; Yenisei—41 dollars, Tuvinsk—67 dollars, Kamchatka—190 dollars, Yakutsk—300 dollars, and the Barguzinsk—405 dollars per skin hide (B.A. Kuznetsov). Ratio, 1:14.4. This example is a utilitarian demonstration of the reality of geographic race.



528 Fig. 202. Reconstructed species range* of sable Martes (Martes) zibellina L. Dashed line designates region in Lithuania and Byelorussia relative to which literature data exist on occurrence of sable in the past. V.G. Heptner.

In the sable very wide individual variation in color is characteristic (see above), and therefore the study of its geographic variation is a very difficult task, and racial characteristics are sometimes ill-defined. At the same time, analysis of a mass of collected material, which has become possible especially in recent years in connection with growth in the number of sables, showed that individual populations of the species differ from each other in percentage of various color types.

^{*}Japanese populations south of Hokkaido are now considered a separate species, M. melampus—Sci. Ed.

In the literature, it was frequently suggested, mainly on the basis of information from hunters and traders, that sable color in one narrow region changes depending on the land inhabited (nut pine—broad-leaved forest), altitude (valleys—mountains) and other ecological conditions, and even annual character of food. Zoologically these observations have not been confirmed; however, to completely deny a connection between characteristics and known ecological conditions is not suitable. This is clear, for example, from those changes in the character of fur in different climates. However, their influence is only revealed over broad areas, for instance in montane and plains countries (see below), but not in individual restricted places as was sometimes indicated (at various altitudes, for example).

The present scheme of geographic variation in sable was made on the basis of very extensive material—of skulls and, chiefly, large quantities of commercial skins (many thousands). It quite clearly reflects the views of furriers on the types of sable, but, from a zoological viewpoint, still cannot be considered exact. Some forms are very subtle or doubtful. Though acceptable in the fur business, they do not qualify as representatives of geographic races in zoology, especially in a stricter and broader interpretation of this concept. Some forms were only defined on the basis of negligible differences in the percentage presence of the three main color types, which, as mentioned above, are generally far from always stable. Some forms will, undoubtedly, be combined.

On the other hand, it is necessary to have in mind some special conditions of existence in the sable. This animal is an animal distinguished by its great attachment to place within a quite strictly delineated locality. Its range under natural conditions, was always broken into separate more or less isolated parts, especially in the east. In the past century, in connection with its extermination, it was divided into small parts, surviving—in places for a long time—without connection with each other. All this may have influenced the formation of small local populations. Easiest of all, in this sense, change in the ratio of color types can be expected. In some cases, separate names were noted, apparently, for local population ("colonial") deviations.

Parallel to this, undoubtedly, sable gives entirely defined geographical forms, irreproachable from a zoological point of view, and well characterized both by color and meristic characters. Such



Plate 5. Barguzin sable, Martes (Martes) zibellina princeps Bir. Painting by A.N. Komarov.



are the Tobol'sk, Altai, Barguzin, Sakhalin, Kamchatka and some others (see below). The reality of geographic forms of sable are found expressed in such a unique index as the value of skins. The skin price of the most expensive category (Barguzin) constitutes about 1450% of the price of the cheapest (Tobol'sk, see page 788).

Some general tendencies may be noted in changes of separate characters. Thus, the largest sables are encountered to the west (Ob' lowlands, Altai) and easternmost parts of the range (Kamchatka, Anadyr Territory). Central and southeastern parts are inhabited by sables of moderate and small size. The silkiest fur occurs in the sables from Trans-Baikalia and Yakutia, and the degree of fineness of the fur falls towards the western and eastern margins of the range and at the periphery, it becomes coarse. This manifestation of general regularity is mentioned by furriers—the coarsening of the fur in more humid regions, especially in districts with a maritime climate. The darkest sables inhabit the central part of the range and the lightest—its margins (Ob' lowland, Sakhalin, Shantar islands). In montane regions, sable are darker than on the plains (Kuznetsov, 1941).

As is clear from what has been said above, the scheme of subspecies presented below is preliminary. It is given as material for further use, after Nadeev and Timofeev (1955) and several other sources. The material studied by the first two authors included 856 skulls, 1000 body measurements and 10,100 skins examined. Since the dimensions of the different described races of sable are quite similar, dimensions are given of the three extreme forms in the morphological and geographical sense (for information on the remainder, see Kuznetsov, 1941; Nadeev and Timofeev, 1955). Data on weights of sable are given at the end of the list of races.

1. Tobol'sk sable, M. (M.) z. zibellina Linnaeus, 1758.

Dimensions large. Fur color light, ranging from gray-brownish to tawny-straw.

Body length of males, 415–520 mm, females, 370–488 mm; tail length of males, 125–190 mm, females, 115–170 mm; length of hind foot of males, 81–110 mm, females, 75–96 mm; height of ear of males, 45–57 mm, females, 43–55 mm. Weight of males, 1000–1780 g, females, 760–1115 g (Pavlinin, 1963; from extensive original data and literature).

Condylobasal length of skull of males (159 samples) 79.7–M 85.7–90.6 mm, females (87) 73.8–M 78.9–83.8 mm; zygomatic

width of males, 44.1-M 48.0-54.8 mm, females 39.0-M 43.6-47.2 mm; height of male skull 29.5-M 32.4-35.0 mm; females 27.4-M29.8-32.2 mm (Pavlinin, 1963).

Golovka and Podgolovka sorts are absent, Vorotovaya constitutes 40% and Mekhovaya 60% [see pp. 763-764].

Found in Pechora basin, North and Middle Urals, western Siberia to Ob' river.

Absent outside USSR.

Lightest colored of all our sables. It is suggested that the Pechora or Pechora-Ural sable differs from the Trans-Ural. At the same time, it is possible that this form occupies West Siberia as far as the Yenisei.

2. Kuznetsk sable, M. (M.) z. tomensis Nadejev et Timofejev, 1955.

Smaller than Tobol'sk sable. Color considerably darker than Tobol'sk form and somewhat darker than Angarsk, but lighter than Altai.

Golovka and Podgolovka sorts constitute 19%, Vorotovaya type 41.9% and Mekhovaya 46.1%.

Found in the western slopes of Kuznetsk Altai, Tom' [river] system.

Absent outside USSR.

3. Altai sable, M. (M.) z. averini Bashanov, 1943 (synonym altaica).

Body and skull dimensions comparatively large, color quite dark and varies from sandy-yellow to dark brown.

Golovka and Podgolovka sorts 26%, Vorotovaya 66% and Mekhovaya 8% (n=1000).

Found in Altai, particularly Bukhtarma basin, northeastern part of Tuvinsk ASSR (Kemchug basin).

Outside USSR, found in southern slopes of Mongolian Altai (Bulugun river).

In several places in Altai, Barguzin sable was introduced, yielding hybrids with local sable.

4. Yenisei sable, M. (M.) z. jeniseensis Ognev, 1925.

Similar to Tobol'sk, but differs in smaller skull dimensions and darker fur color. Fur is loose, but very coarse.

Found in interfluve of Ob' and Yenisei rivers from northern border of taiga southwards to Chulym river.

Absent outside USSR.

5. Angara sable, M. (M.) z. angarensis Nadejev et Timofejev, 1955.

Differs from Yenisei in smaller average skull dimensions. General color comparatively light, but noticeably darker than Tobol'sk and Yenisei.

Golovka and Podgolovka sorts constitute 9.7%, Vorotovaya 77.8% and Mekhovaya 12.5% (n = 2600).

Found from Yenisei valley eastward to Oka (tributary of Angara river), along right bank of Angara northward to watershed with Podkamennaya Tunguska and southward to Kansk steppe.

Absent outside USSR.

6. Sayan sable, M. (M.) z. sajanensis Ognev, 1925.

Differs from Angara by considerably darker color. General tone of fur tawny-brownish with admixture of pale-straw underfur.

Golovka and Podgolovka categories constitute 17.4%. Vorotovaya 70.9% and Mekhovaya 11.7% (n = 2679).

Found in Sayans.

Outside USSR, found in Kosogol lake district in Mongolia.

7. Tungusska sable, M. (M.) z. tungussensis Kusnetzov, 1941.

Differs from Tobol'sk in less massive skull, somewhat shorter braincase and considerably darker fur.

Golovka and Podgolovka sorts constitute 6%, Vorotovaya 55% and Mekhovaya 40%.

Found in basins of Podkamennaya and left tributaries of Nizhnaya Tungusska.

Absent outside USSR.

8. Ilimpiisk sable, M. (M.) z. ilimpiensis Nadejev et Timofejev, 1955.

Similar to preceding form in body and skull dimensions but differs by its considerably darker color.

Golovka and Podgolovka sorts constitute 16%, Vorotovaya 53%, and Mekhovaya 31% (n = 2600).

Found north of Nizhnaya Tungusska to northern border of species range, and eastward from Vivi to Lena, southern border between 64° and 64° N. lat. Taiga of Tura, Kureika, Kotyi, and Anabar basins and upper reaches of Olenek.

9. Barguzin sable, M. (M.) [z.] princeps Birula, 1922 (synonym baicalensis).

Dimensions relatively small—one of smallest races of species; color entirely dark, but overall somewhat lighter than Vitim sable.

Body length of males, 394–M 415–420 mm, females, 360–M 382–410 mm; tail length of males, 122–M 144–155 mm, females, 120–M 129–145 mm; condylobasal length of males, 73.9–M 77.9–81.0 mm, females, 68.4–M 73.1–79.1 mm; zygomatic width of males, 39.6–M 41.6–44.5 mm, females, 37.7 M–39.7–41.8 mm; height of male skull, 29.6–M 30.5–32.3 mm, females, 28.5–M 29.7–31.4 mm.

Golovka and Podgolovka sorts constitute 45%, Vorotovaya 46% and Mekhovaya 9% (n=786).

Found on eastern shore of [Lake] Baikal; Barguzin range from right tributaries of Barguzin to watershed with upper Angara.

Absent outside USSR.

One of the most valuable forms.

10. Vitim sable, M. (M.) z. vitimensis Nadejev et Timofejev, 1955.

Larger than Barguzin, but smaller than Tobol'sk, Altai, Kamchatka and Chikoisk. Color is darker than in Barguzin, very dark, intense blackish-brown. Throat spot weakly defined. Fur fluffier and silkier than Barguzin.

Golovka and Podgolovka sorts constitute 56%, Vorotovaya 42% and Mekhovaya 2% (n=5529).

Found on right banks of Kirenga and Lena, upper Vitim and upper Angara and northern extremity of Baikal.

Absent outside USSR.

Form closest to Barguzin. One of most valuable.

11. Chikoisk sable, M. (M.) z. obscura Nadejev et Timofejev, 1955.

Darkest form, considerably darker than Barguzin. One of large forms, inferior only to Tobol'sk, Altai and Kamchatka.

Golovka and Podgolovka sorts constitute 71%, Vorotovaya 27.6% and Mekhovaya 0.9% (n = 483).

Found in southeastern extremity of Yablonovoi range—Chikoi system, the right tributaries of Selenga and Ingoda.

Outside USSR—Kentei [mountains] in Mongolian Republic. Extremely valuable form.

12. Yakutsk sable, M. (M.) z. jacutensis Novikov, 1956.

Dimensions particularly small, smallest race of species in USSR. Pelage very fluffy and silky. Color strongly variable, but the dark sables prevail.

Golovka and Podgolovka sorts constitute 53%, Vorotovaya 42% and Mekhovaya 5% (Kuznetsov, 1941).

Found in upper Aldan and Zeya eastward to Uda.

Absent outside USSR.

For naming of form, see synonymy of species.

13. Sakhalin sable, M. (M.) z. sahalinensis Ognev, 1925.

Dimensions very small, color very light with predominance of reddish tints.

Golovka and Podgolovka sorts constitute 4%, Vorotovaya 59% and Mekhovaya 47% (Kuznetsov, 1941).

Found in Sakhalin [Island].

Absent outside USSR.

It is probable, the name *brachyura* belongs to the form since, according to some data, Temminck described this form from skins obtained from Sakhalin. Relationship of Sakhalin sable to that of Hokkaido (*brachyura*) is not clear.

14. Ussuri sable, M. (M.) z. arsenjevi Kusnetzov, 1941.

Dimensions as in Sakhalin sable, color medium dark, pelage less fluffy, as if clipped, but soft and fine.

Golovka and Podgolovka sorts constitute 16%, Vorotovaya 67% and Mekhovaya 17%.

Found in Ussuri Territory, mainly in Sikhote-Alin' taiga.

Outside USSR, found in contiguous parts of North-east China.

Relationship of this form to form *coreenis* (hamgyensis) found in Korean Peninsula needs clarification.

15. Shantar sable, *M.* (*M.*) *z. schantaricus* Kusnetzov, 1941. Dimensions as in Ussuri sable. Color darker than Sakhalin and Ussuri. Pelage quite fluffy.

Golovka and Podgolovka sorts constitute 32%, Vorotovaya 63% and Mekhovaya 5%.

Found in Shantar Islands, the basin of lower course of Amur and Tuguro-Udsk coast of Okhotsk Sea.

Absent outside the USSR.

16. Kamchatka sable, M. (M.) z. kamtschadalica Birula, 1918 (synonym kamtschatica).

Distinguished by large dimensions of body and skull—largest form of species. Color strongly variable, but dark individuals predominate. Pelage very thick, but insufficiently soft.

Body length of males, 445–M 490–580 mm, females, 415, M 448–510 mm; tail length of males, 147, M 160–175 mm, females, 132, M 152–172 mm; condylobasal length of male skull, 85.6, M 90.4–94.6 mm (M 88.5 mm–93), females, 79–4, M 82.1–

84.4 mm (M 80.8 mm-76); zygomatic width of males, 51.3, M 53.5-56.2 mm (M 50.2 mm-81), females, 43.6, M 46.3-52.8 mm (M 44.9 mm-74); skull height of males, 31.6, M 33.5-35.1 mm (M 33.3 mm-94), females, 29.8, M 31.5-39.6 mm (M 30.6 mm-75) (Timofeev and Nadeev, 1955, from 56 skulls; in parentheses, mean and number of individuals from Kuznetsov, 1941).

Golovka and Podgolovka sorts constitute 16.0%, Vorotovaya 76.0% and Mekhovaya 8.0%.

Found in Kamchatka and Koryak land in the Apuka basin. Absent outside USSR.

17. Kuril sable, M. (M.) z. brachyura Temminck, 1840.

Diagnostic features of sable found in the Kuril Islands are not sufficiently clear. Some authors relate its name to the named Japanese form. Apparently, it belongs to the Sakhalin in sable type.

On the whole, all forms enumerated may be regarded as aggregating into seven groups (large populations): Tobol'sk—Pechora, Urals and West Siberia to Yenisei; Altai [and]; Sayan—Tuvinsk ASSR, Sayans and north to Kuznetsk Altai; Yenisei—right bank of Yenisei to Lena; Trans-Baikaliya—south to border of species range, east to watershed of Zeya and Bureya, north, including Vitim; Sakhalin—lower Amur, Sakhalin, Ussuri Territory and Shantar Islands; Kamchatka—Kamchatka and Koryak land (B.A. Kuznetsov).

Weight of sables from various parts of the range is as follows (Kuznetsov, 1941): Yenisei sable—males (93) 1030, M 1307–1500 g, females (125) 880, M 1182–1250 g; Sayan sable—July males (22) 1200, M 1433–1800 g, females (21) 870, M 980–1300 g, January males (22) 1110, M 1472–1810 g, females (21) 820, M 1132–1560 g; Sakhalin sable—July males (22) 940, M 1239–1600 g, females (25) 800, M905–1130 g, January males (22) 880, M 1193–1500g, females (25) 740, M 916–1120 g; Kamchatka sable—males (4) 800, M about 1500–1869 g, females (5) 600, M about 1100–1140 g.

Outside the limits of the USSR, the following forms are noted (sometimes, several of them are related to "M. melampus"): 1) M. z. brachyura Temminck, 1844—in Hokkaido, Japan; 2) M. (M.) z. melampus Wagner, 1840—in Honshu (Hondo), Shikoku, Kyushu—Japan; 3) M. (M.) z. tsuensis Thomas, 1897—in Tsushima Island in the Korean strait; 4) M. (M.) z. koreensis Kuroda et Mori, 1923 (synonym hamgyensis, Korean Peninsula) (V.H.).

Biology

Population. By the 30's of the 20th century the number of sable had become very small as a result of their rapacious destruction for about a whole century; at the present time their numbers are continuously increasing, as a result of the system of state measures for protection and restoration of this very valuable fur-bearing animal and they far exceed the prerevolutionary.

At the present time, there are many regions in Siberia where the population density of sable attained a level which previously seemed impossible and was not actually present. The latter is explained in that nowhere in the past within the range of the sable, were there territories which were released due to scarcity of sable hunters. In connection with this, in many places, areas were overpopulated by sables that led to undesirable consequences. Such saturation could only occur in the period before the appearance of the fur trade.

The present number of sable has already for some time allowed the establishment of a planned, licenced harvest. Sable are quite unevenly distributed within the limits of their range. This condition is due not only to different degrees of favorable environmental conditions but also to the fact that in the different parts of the range the active measures for restoration of its numbers were begun at different times. Therefore, at present the number and density of sable still do not correspond everywhere to the capacity of taiga areas and its distribution is not the result of natural regulation. Evaluated on the results of the hunting harvest, the total number of sable in the USSR could be very provisionally calculated to be about 500,000.

For the greater part of the present range, the average density does not exceed 1.5 animals per 10 km² (Sverdlovsk, Tyumen, Kemerov, Irkutsk, and Chita oblasts, Buryat ASSR, Kamchatka). In places, this density is considerably lower (Omsk, Tomsk, Amur oblasts, Tuvinsk ASSR and others). In individual regions (Eastern Sayan, Altai and others) the average density reaches 2.5–5.0 and 10–12 individuals per 1000 hectares (Nadeev, 1961). In southern Altai, in areas of highest sable density, one sable has 3 km² (3.3 sables in 1000 hectares), while in the areas that are regularly exploited—4.2 km² (Afanas'ev, 1961).

In Kamchatka, in the best areas (forests of Erman's birch [B. ermani], mixed broad-leaved-fir-birch forests), density reaches 1.5–2.0 sables per 10 km², with 8.3–8.5 track encounters per 10 km in good areas (forests of white birch [B. alba], flooded forests)—1.4 (6.8–7.3 track encounters), in moderate (broad-leaved and fir forests)—1.3 (4.8 track encounters) and in the worse—0.1–0.3 (0.8–1.4 track encounters). The total number of Kamchatka sables is estimated at 19,000 (average catch is 7,650 individuals, equaling an average growth of 40.3%; A.A. Vershinin).

In northwestern Yakutia, one sable has 15–26 km² and taking into consideration uninhabited regions—100–120 km² (Tavrovskii, 1958).

However, contemporary census methods are unreliable and often extrapolated over large areas with insufficient basis.

Habitat. Sables inhabit large massifs of northern coniferous forests of the taiga type. They are in equal measure native to montane and plains taiga (urman)*, penetrating to the zone of sparse tree growth in the north and in the mountains. They do not go beyond the limits of coniferous taiga. They avoid cultivated areas, and cross their boundaries only during times of migration. Preference is shown for dark coniferous plantations almost always having in their composition Siberian stone pine. This is because of the great availability of food (pine-nuts, forest voles) and the protective nature of this plant formation.

Only as a result of irrational utilization, sable became mainly inhabitants of montane taiga, rocky talus and frequently even montane balds. At the present time, in the same way as in the distant past, sable willingly occupy and attain considerable density where lowland pine forests and swamps predominate, although even here, they prefer the islands of nut-pine and spruce forests, margins of moss bogs and narrow belts of dark coniferous forests along river banks. Sable also lives under unique conditions such as montane forests of Erman's birch in Kamchatka, in larch forest with an understory of green alder [A. viridis] in the Zhigansk region and even in forest tundra in the Gizhiga and Penzhina regions.

The close linkage of sable with the Siberian nut-pine is exclusively conditioned by the general scarcity of food available for it

^{*}Local word-Sci. Ed.

in the Siberian taiga. This connection is not an indispensable condition of its existence.

Food. The sable is a polyphagus carnivore. In addition to warmblooded animals, plant food—seeds of Siberian and Korean nutpine and prostrate nut-pine, berries and insects are of great significance in its food. The composition of its food varies greatly in various places. For example, differences in food type of lowland and montane sables are quantifiable. As in pine marten, sable foods reveal geographical, stand-type and sexual differences. The larger and stronger males often consume larger prey—capercaillie, blackcock, and white hares. Such differences in nutrition were noticed in the foothills of the East Sayans (Dul'keiti, 1956). They are also confirmed in the northern Urals (Zaleker and Poluzadov, 1955) as well as for the Yenisei sable (Kiris, 1953). However, several investigators did not find these differences (Raevskii, 1947; Lavrov, 1953). This can be explained easily in that in many



Fig. 203. Habitat of sable in sparse growth of montane nut-pines at the upper limit of forest. Altai preserve. Photograph by G.D. Dul'keit.

regions, large food objects are absent or are met with rarely and sporadically.

In the northeastern Pribaikal, Khabarovsk Territory and a series of other regions, only two elements—forest voles and pinenuts—or the forest voles and cowberry [V. vitis-idaea]—are of essential significance in sable nutrition.

The geographical and seasonal changes in sable foods are well manifested (see Tables 50, 51). For Kamchatka, the willow ptarmigan, root vole, "nuts" of prostrate nut-pine and fish are characteristic foods. Red-backed voles, pine "nuts" and mountain ash predominate in foods of the Barguzin sable. For Kondo-Sos'vinsk sable, capercaillie and, in general, tetraonid birds are typically the most often encountered, and for Pri-Amur sable—forest voles and cowberry.



Fig. 204. Taiga along Mana river—a tributary of the Yenisei, habitat of sable. "Stolby" preserve south of Krasnoyarsk. Photograph by G.D. Dul'keit.

The food composition of sable changes in different years depending upon yields. With failure of the plant food crop, the role of warm-blooded animals significantly increases and vice-versa (Shaposhnikov, 1956). A lessening of the role of one of the foods causes increased consumption of another. Usually, a deficiency of one or two main food is compensated by the utilization of secondary foods, or those which are not regularly utilized.

Food composition is not the same even between small populations living in separate montane valleys in one region. This is well illustrated by data from the Barguzin preserve (N.M. Baevskaya) (Table 49).

Table 49. Food composition of populations living along different rivers in Barguzin preserve (occurrence in %)

Food composition	Bol'shaya river	Davshe river	Tarkulik river	
Mouselike rodents	90.0	75.0	92.3	
Birds	13.0	7.5	3.8	
Reptiles	12.2	5.0	3.8	
Insects	23.6	25.0	15.3	
Pine "nuts"	30.0	55.0	73.0	
Berries	16.9	20.0	3.8	

Food composition of sable changes in snowy and nonsnowy periods of the year in various parts of the range (Tables 50, 51).

The seasonal variations in sable nutrition are not as sharply manifested as in the pine marten. They are determined by the seasonality of a series of foods—insects, berries, and nuts, which can serve as food for sable only in the warm period of the year. In Kamchatka, fish becomes available for sable only in the salmon spawning period. On the other hand, seasonality determines the availability of food for sable; therefore, in the snow-free period, forest voles, especially gray [C. rufocanus], wood lemmings [L. schisticolor], shrews and Siberian chipmunk are significantly more available than in the snowy period. In this sense, winters with deep snow and those with little snow differ from each other. In winters with deep snow, sables more frequently catch tetraonid birdscapercailles and hazelhens—when they spend the night under snow. In winter periods with deep snow, sable feed mainly on berries of mountain ash, and in autumn, or when there is little snow-on cowberry, and in summer, on blueberry. Deep snow makes it difficult to obtain voles, pine "nuts" and some other food.

Table 50. Geographic variation in sable foods in the snow-free period of the year (occurrence in%).

Region, Number of items, Investigator	West Siberian lowlands	Northeastern Altai	Barguzin preserve	Middle Sakhalin
Food composition	Raevskii, 1947	76 Shaposhnikov, 1956	314 Timofeev, 1948	357 E. Volkova
Forest voles	57.7	36.8	73.5	64.0
Siberian chipmunk		3.9	3.5	5.0
Eurasian flying-squirrel	·	1.3	2.5	1.0
Common squirrel	7.7	3.9	_	0.2
*Pika		0.5	1.9	
Shrews	7.7	19.7	13.0	2.0
Birds	23.1	1.0	6.9	25.0
Tetraonids	7.7	3.9	1.2 No	information
Hazel hen	7.7		1.2 No	information
Bird eggs	3.8	1.3	0.6	0.6
Insects	53.8	13.1	5.7	15.0
Pine "nuts"	3.8	36.8	37.6	34.0
Berries	44.5	13.1	35.7	66.0

*The Russian word senostavka ("haystacker") is used, rather than the more common pishchuka—Sci. Ed.

Sable eat carrion and the food remains of other carnivores—this explains, for example the occurrence of squirrel in the food of sable (Shaposhnikov, 1956; P.P. Tarasov).

Utilization of the Eurasian flying-squirrel [Pteromys volans] is associated with diurnal activity of sable; the latter can overtake it in its holes only during the day (the flying squirrel is a nocturnal animal).

In Kamchatka, the frequency of the most important food component—voles—varied in different years from 35% to 84% (A.A. Vershinin) (Table 52).

Summing up the factual data on sable foods, one may affirm that the significance of the Siberian chipmunk in its food is extremely limited and is not found everywhere: in summer, its occurrence in sable food does not exceed 3–5% and in winter, is even less. The old idea about the great significance of haystackers (pikas) in sable nutrition is not confirmed. In winter foods, the share of pikas (by percent of occurrence) ranges from 0.9 to 10.1%, more usually not exceeding 5%. In summer it is still less. Pikas occur in sable foods in only 46% of the regions where its nutrition has been

Table 51. Geographic variation in sable foods in the snowy period of the year (% of occurrence)

ii Sikhote- Middle 5- Alin' Sakhalin 5k	37 22 Bromlei, E.P. ov 1956 Volkova		18.9 9.0 10.8 9.0 5.4 N.L* 5.4 N.L*	5.4
Nizhnii 1 Gorino- k Kurinsk region	227 39 Tavrov- G.K. skii, 1958 Abramov	61.5	111.5	15.4
North- western Yakutsk		34.7 8.4 8.4 — 10.1 1.7 5.9	33.9 27.9 — 27.9	24.8
Bol'shoi Shantar Island	152 Dul'keit, 1958	71.7 2.0 7.9	3.9	- 0.7
Center and south	150 Various authors	57.0	20.3	7.0
Kamchatka Karachi- Cer msk and ar Tigil'sk sou regions	107 Lavrov, 1953	27.1 39.2 16.8 0.9	38.3	1.9 34.6 41.0
North- eastern Pri-Baikal, Barguzin	149 521 Dul'keit, Timofeev, 1956 1948	45.8 0.3 5.1 1.9 2.3 0.5	2.5	66.7
Cismon- tane Sayans	149 Dul'keit, 1956	59.7	8.1 2.1 0.7 1.4	98.7
Irkutsk oblast	122 Kiris, 1953	22.4 13.7 13.6 1.0 1.9 1.0	14.6	33.0
North- eastern Altai	340 Shaposh- nikov, 1956	32.9 15.7 11.3 2.5 5.2	3.4 15.9 5.9 0.2 5.6	26.5
West Siberian Iowland	150 Raevskii, 1947	78.7	27.5 10.8 5.3 2.2	63.3
North Urals, Ivdel'sk region	132 Zale- ker and Poluzadov, 1959	21:2 43:9 6.8 — — 4.8 10:3	18.5 10.3 N.I.* * X.I.X N.I.* * X.I.X	0.7
Region, Number of items, Investigator	Food	Forest voles Other voles Shrews Siberian chipmunk Pika Squirrel White hare	Eurasian flying squirrel Birds Tetronid birds Capercaillie Hazel hen	ptarmigan Fish Pine "nuts" Berries

* No. Information

Table 52. Results of a multiyear study of materials concerning sable nutrition in Kamchatka (1409 stomachs; A.A. Vershinin)

Food composition	Occurrence (in %)	Specific weight of individual foods	
Mammals	69.8	66.6	
Voles	61.1	61.0	
Root voles [Microtus oeconomus]	24.0	24.0	
Red-backed voles [Clethrionomys	rutilus] 20.4	12.7	
Red-gray vole [C. rufocanus]	16.5	19.4	
Squirrel [Sciurus vulgaris]	0.8	0.4	
White hare [Lepus timidus]	2.7	2.4	
Pika [Ochotona hyperborea]	0.4	_	
Birds	20.8	6.1	
Capercaillie [Tetrao parvirostris]	1.7	1.2	
Willow and rock ptarmigan	1.5	1.2	
Small birds	12.5	3.6	
Bird eggs	1.1	_	
Fish	18.1	11.9	
Salmon	10.2	-	
Insects	2.5	_	
Hymenopterous insects	0.9	_	
Plant food	53.5	15.2	
"Nutlets" of prostrate nut pine	10.3	2.7	
Berries	_	12.5	
Mountain ash [Sorbus]	21.6	3.6	
Hawthorn [Crataegus]	20.9	6.1	
Chokecherry [Prunus sp.]	4.8	_	
Rose [Rosa sp.]	7.3	_	

studied. The percentage of squirrel occurring in winter foods of sable ranges from 0.2 to 11.3%, averaging 3.5%. In the summer period, it ranges from 0.2 to 7.7% (on average 2.9%).

As a result of data communicated on the significance of squirrel in sable nutrition (Timofeev, 1962) it was revealed that in various parts of the range and in various years, the percentage of occurrence of squirrel in stomachs and extrement of sable varied from 0 and 26%; on average, 4.4%. Of 33 data series, the percentage of squirrel occurrence was more than 10% in only 6 cases. It may be considered that: 1) The role of squirrel in the diet of sable in different years and seasons is not the same and is not connected with degree of squirrel abundance in areas inhabited by sable; 2) this role increases in the periods of scarcity of other main foods of sable (voles, pine "nuts"); 3) sables catch squirrel mainly on the ground; pursuit of squirrels in the tops of trees end unsuccessfully in most cases; 4) destruction of small squirrels in the nest is not

yet proven, 5) the influence of sable on reduction in number of squirrels is not so great that it can explain reductions in the resulting squirrel harvest. These far from complete data indicate that squirrel is of secondary importance or even an accidental element in sable nutrition.

The sable cannot penetrate into the burrows of pika and chipmunk due to its large size. In winter, the chipmunk sleeps deep inside its burrow, and even the brown bear cannot dig it out. However, in summer sables catch chipmunks by ambush in the same way as it does with pika. In winter, pikas come out of their burrows with their hay stores under the snow where they are sometimes overtaken by sable. Sable catch tetraonid birds in their snow burrows, but this does not occur often. In the north Urals, the sable and kida catch one tetraonid for every 10–15 attempts, when the birds succeed in flying away.

In captivity, when offered 200 to 300 g food, sable did not eat it all, but hid some (Dul'keit, 1929); a norm of 170-180 g and 150-160 g of food were sufficient for males and females respectively. Under natural conditions, pine marten and sable do not eat more than 1/10 of their live weight per day, usually 100-170 g (P.B. Yurgenson; Timofeev, 1951). They usually leave food behind, when food can be obtained in abundance. Concerning the statement (Petryaev, 1950), that sable eat in one day an amount of food equal to half its live weight, we consider it impossible. The volume of the sable stomach does not exceed 120 to 200 cm³ (Sokolov, 1941), and in nature a full stomach was practically never found in sable. In Kamchatka, the maximum weight of stomach contents in sable was established as 36 g with an average of 24.4 g. In that study, in one stomach up to 6 voles, 500 "nutlets" of dwarf pine, 160 fruits of mountain ash, 50—rose, and up to 300 hawthorn, were found at one time.

Differences in the sable diet may be observed in individuals of different sex: in females, the percentage of empty stomachs is 56.6 and in males—52.7, and the average weight of stomach contents is 22 g and 26.4 g respectively, and fatness in females is also less. Young (yearling) sables also feed less well. Sable diets differ in separate regions of Kamchatka and in different years (A.A. Vershinin).

The sable does not make food caches. In the presence of large prey, it makes a temporary lair nearby.

Home range. In August, the sable litter disperses. Young sables begin to wander, searching for a permanent home range. Food shortage intensifies their wandering. When the period of settlement is completed, sable become strictly sedentary animals. The home range selected is usually used for many years, often until death. Only forest fire, felling of the forest and similar events make the sable leave its home range. After the death of the "owner", another one occupies the range, preserving its boundaries which are determined by the boundaries of the home ranges of neighboring sables (Raevskii, 1947). Within each range, only one animal, or a female and her litter, live. With significant population density, however, neighboring home ranges often impinge on one another. Occasions have been observed when the owner of a home range pursued and drove away from its boundary another sable that had penetrated thence. Rarely, fights may also occur, usually during low densities. More often, sables avoid transgressing into the range of their neighbor, limiting themselves to their peripheries.

In case of high density, it seems as though the reflex of range defense is lost. Competition is not intensified, but migration appears, mainly among juveniles—the less settled part of the population (O.K. Gusev²⁵).

The size of the home range is determined by the abundance of food, the presence of escape and nesting conditions, and also the percentage correlation inside the home range area of various qualitative factors including those which are not all necessary for the sable. Each home range seems to be divided into separate sections of daily activity which are periodically visited by the sable. Sometimes, within the boundaries of such a range it will stay for some days, whereas others are not visited for a long time.

The areal dimensions of the home range, equally with the length of the daily movements, are the best criteria (bonité) for the quality of sable range. In the American sable [= marten, *Martes americana*] length of daily movement in the USA is equal to 8.4 km on the average, varying from 3.2 to 14.4 km. Correspondingly, the range of daily activity equals 248 ha on the average, varying from 129 to 518 ha (Marshall, 1951). By periodically changing

²⁵There exists the opinion (Raevskii, 1947) that excess individuals inhabiting the central parts of a densely settled territory die as a result of intensive competition since such sable do not have the rank to take over ranges inhabited by other individuals. Later (Tavrovskii, 1958), it was shown that this opinion is mistaken.



541 Fig. 205. Littered montane taiga in the "Stolby" preserve (Western Sayans south of Krasnoyarsk). Place of day-time lair of sable in areas where Barguzin sable was introduced. Photograph by G.D. Dul'keit.

these ranges, one animal may occupy a home range of 2590–3885 ha (states of Idaho and Montana). The size of the daily range of American marten in Glacier National Park (Montana) is 233 ha on average for males (77.7–440.3 ha) and for females—69.9 ha (7.7–181.3 ha). Through repeated tracing of the tracks of one male, daily length [of the track] was about 0.8 km, varying from 0[.0] to 12.5 km. As in Siberian sable, the borders of the range usually intersect each other (Vernon, Hawley, 1957)*.

In Kamchatka, the size of the home range rarely exceeds 10 km² (Plechev, 1939), on Bol'shoi Shantar Island, on average 13 km² (from 5 to 30 km) (Dul'keit, 1929). In the Zhigansk region (Yakutiya), home range comprises about 30 km² (Romanov, 1938). In northwestern Yakutiya (Tavrovskii, 1958), 5 out of 8 sable trails

^{*}Correct citation is Hawley, V.[ernon], 1957—Sci. Ed.

did not exceed a circle 4 km in diameter (about 12.6 km²), in eastern Sayan—from 4 to 10 km² (Kozhanchikovy, 1924), on the northeastern shore of Baikal—about 10 km² (Doppel'mair, 1926), in the upper Katun' river (Altai)—from 8 to 12–15 km² (V.V. Dmitriev and P. Bashilov), in the former Kondo-Sosyvinsk preserve, on average about 10 km² (Raevskii, 1947), and in the north Urals on the upper Ilych river—about 4–6 km². In the Eastern Sayan foothills, in case of a moderate crop of principal food, a home range of 2.5–3.0 km² is sufficient for one sable (Dul'keit, 1957); the maximum density in this case was 1 sable per 2.6–2.7 km².

Within the limits of the distribution that are observed, consequently, there is fluctuation in size of range from 4 to 30 km². Such fluctuations occur locally and in limited territories.

Burrows and shelters. Breeding, winter, autumn and temporary dens may be distinguished (Raevskii, 1947). Breeding and winter dens are permanent. They are usually in the form of dry hollows in trees and stumps and in logs that are not completely lying on the ground, and quite rarely—in holes in the ground and in crevices in rock slides. The nesting chamber is covered with dry grass, lichens, wool, feathers, down, etc. Not much bedding occurs.



Fig. 206. Barguzin sable in a snow lair. "Stolby" preserve south of Krasnoyarsk. Photograph by G.D. Dul'keit.

Winter dens are permanent only where winter is distinguished by its severity. In Kamchatka (V.A. Kotov), in northeastern Altai (Shaposhnikov, 1956) and in Primor'sk Territory (Bromlei, 1956), they are not manifested. Permanent winter nests show signs of significant occupation (ice-covered entrances, excrement, ectoparasites and others). Autumn lairs are characterized by less evidence of occupation: a tree hole. For permanent habitation in winter they are very wet or cold. Temporary and occasional lairs are of various forms. Within the boundary of the home range, the sable has some of these. In the Eastern Sayan foothills, 51% of sable dens in winter were under windfalls, roots and uprooted trees, and 49%—in cliffs, rock slides, and boulders (Dul'keit, 1957).

Daily activity and behavior. The sable belongs among those animals with an indefinitely defined rhythm of daily activity. Individual sables are observed with crepuscular-nocturnal—others with diurnal types of activity. It is not even rare that one and the same animal is active during the day, and then in the twilight and at night, depending upon the success of its hunting, weather conditions and other events. In the northern taiga, in connection with the characteristics of the light regime in the course of the year, the daily rhythm of sable life and its victims is particularly unclear (Raevskii, 1947). In a series of cases, change in the predominant types of daily activity have taken place as a result of intensive pursuit by hunters, who can more easily extirpate animals with a crepuscular-nocturnal type of activity. In specific cases such changes in type of daily activity of a population over a 100-year period may be established by comparing recent data with these of L.P. Sabaneeva (1875).

There is no single rhythm of daily activity in different populations. In the northern and middle Urals and on the shore of 543 Baikal, the diurnal prevails, and in the Trans-Urals—crepuscular-noctural. On B[ol'shoi] Shantar Island and in the northeastern Altai, the animals have no definite rhythm. In the foothills of the Eastern Sayan, in 68% of the cases, sables hunt during the day (Dul'keit, 1957).

The sable is a typical terrestrial carnivore. On trees, it does not feel self-confident, it climbs more poorly than pine marten and is not capable of moving directly from one tree to another as can the latter. Having climbed a tree, it jumps down again. The sable is well adapted to living on the ground surface in severe snowy



543 Fig. 207. Sable in natural habitat. Stolby preserve south of Krasnoyarsk. Photograph by G.D. Dul'keit.

winters. It orients itself well within the subnival space, moving about freely there and capturing food items.

The senses of hearing and smell are well developed. Vision is weak and monochromic. The sable swims well.

In its search for food during a 24-hour period, the sable journeys a quite considerable distance. The length of the daily winter trail depends on the abundance of food and the degree of its availability to the sable, as well as on the type of snow cover and sex of the animal (Dul'keit, 1957). While moving on soft snow, the sable quickly tires. The small size of the female leads to the fact that with the same number of jumps and energy utilized, the female runs a shorter distance than the male.

In the basins of Konda and Sos'va rivers (Raevskii, 1947), the sable moves 2–3 km per day (early in spring, 4–5 km); in the northern Urals (Ivdel'skii region)—8–9 km; in northeastern Altai (Shaposhnikov, 1956)—from 3 to 11.5 km (average, 5.7). In the southern Altai (Kazakhstan), the length of daily trail of the sable ranges from 0.2 to 5 km, usually 3–4 km. During a snowfall, the sable rarely moves more than 2 km (Afanas'ev, 1961). For the Eastern Sayan (Solov'ev 1921), the path is indicated to be about 5 km; in Barguzin preserve—about 10 km on the average; in Kamchatka (Kazarinov, 1946)—about 12–15 km; in the Sikhote-Alin' range (Bromlei, 1956) and in snow 12–14 cm deep—from

1.3 to 3.1 km, averaging 2.4 km. In the foothills of the E[astern] Sayan (Dul'keit, 1957), length of daily sable trails in the 1953-1955 period did not exceed 9.2 km. Average length of the daily trail was 5.6 km for males, and for females-4.5 km. Average length of the daily trails (both sexes) was 5.1 km. In the first half of winter, when it is easier to capture its food, it runs 4.3 km per day, and in the second half of winter-5.9 km. The larger the sable, the longer its trail per day. Deep snow and frost shorten it, 544 as well as abundant food; in years of nut pine harvest, the sable sometimes becomes satiated in a 1-km journey. In northwestern Yakutiya (Tavrovskii, 1958), the average length of the daily journey of the sable is about 4 km. A circular route is characteristic for sable; along its way it rarely doubles back or turns aside. Even while fattening, the sable's path is distinguished by its characteristic directional integrity. In winter, the sable catches mouse-like rodents under the snow; on warmer days, they often ambush them on the surface of the snow like a cat (northeastern Altai: Timofeev, 1951; Shaposhnikov, 1956). It catches tetraonid birds in the snow holes where they spend the night. It searches for nut pine "nutlets" and cowherries under the snow. Mountain ash berries are eaten directly from the branches.

Seasonal migration and transgressions. The sable is a sedentary animal, but translocations do occur in the species. Above all, there is the yearly dispersal of young in August to a new place, beyond the boundary of the home range where the litter was weaned. The length of such migration in search of a habitat not occupied by sables is determined by the degree of occupation of adjacent areas. With development of harvest, these migrations are not great, in other cases, sables cover a distance of 50–70 km and more.

Older sables ("amans") with worn teeth lead, to a significant degree, a nomadic or seminomadic mode of life. They roam very widely within the limits of their range in search for the most available foods.

For Kamchatka (Vershinin and Dolgorukov, 1947) seasonal migrations are noted above all; annually, in the second half of winter, sables descend from the mountains into the valleys in connection with deepening and compaction of the snow, following hares and ptarmigan.

Significant emigrations occur locally in years with sable food shortages. However, north Ural sable hunters believe that the sable dies in its place and does not leave the region of its inhabitation. Apparently, sable behavior is geographically variable.

Finally, massive displacements of sable are known in cases of eruption of volcanos (Kamchatka) and taiga forest fires in the dry years that sometimes cover vast territories in Siberia. However, in the case of large taiga forest fires, comparatively few sables are saved by fleeing; the majority of them die from the fire. Apparently, massive migrations due to food shortage is possible. In the Sayans, they were noted in 1875, 1888, 1900, 1915, etc., approximately every 12 to 15 years. This question is not yet well studied.

Sables tagged in the northern Urals were caught at distances of 2.0; 2.0; 4.0 and 4.5 km from the point of release (Raevskii, 1947). One tagged sable was caught after 8 years 20 km from the place of release (Nadeev and Timofeev, 1955).

Dispersal of young sables sometimes takes place in groups (litters?), in which one sex often predominates (Dul'keit,1957). The length of daily trails of dispersing sables reaches 10 km and more, the animals moving with longer jumps than during the fattening period. With increase in snow depth, dispersal stops. Areas from which sables disperse are usually those which are not fully exploited. They settle in areas where sables were removed during the harvest period.

In Glacier National Park in the USA, in an experimental area of 1,554 hectares, 85 sables [=American marten] were marked and repeatedly trapped; 54 males and 31 females were caught 525 times, *i.e.* an average of six times each; 57.6% of the sables were caught not less than two times, and one male was caught 73 times during 562 days. Only 27 sables were entirely settled. Thirty individuals stayed in a place for more than three months, nine individuals—from one week to three months and 47 sables were transients.

Reproduction. In cage raising, the main mass of sables attain sexual maturity at the age of 2 years and 3 months. At the age of 15 months, 16% of the females become sexually mature (Starkov, 1947). In Pushkin state fur farm, 10% attain sexual maturity in the second year, 70–80%—in the third year; the remaining animals—in the fourth year or they do not reproduce at all (Nadeev and Timofeev, 1955). Termination of sexual activity is observed there at 13 years; individual females remain fertile until 15 years old. At 16–17 years, non-productive attempts at reproduction still occur. Of nine females older than 10 years, only one exhibited senile changes of the sex organs, but the old females are usually less fertile. In captivity, sable live for about 15–18 years.

The least percentage of infertility was observed between 5 and 8 years (Starkov, 1947). During the ages of 4–9 years, the average number of young in a litter is 3.5–3.6 and by 15 years, falls to 1.5.

In nature, the majority of females, according to data from histological investigations, become pregnant in the second year of life (Zaleker, 1953). The percentage of pregnant females among Barguzin sables in the second year of life in nature was from 26 to 33% (Baevskii, 1956). In adult females, it ranged from 50 to 72.9% depending on nutritional conditions in the data year. In regions of intensive exploitation, infertility among females was higher (72% as against 50%), while among young females, pregnancy was not observed at all. The percentage of pregnant females among different geographical populations ranged from 88 to 100% in 6 different regions (Zaleker, 1953).

In Kamchatka from 1952–1962, of 795 females 46.2% were pregnant, among second-year females—27.5%, among third-year females—46.3%, and among older females—62.5%, and in very old females—20%. Percentage of pregnancy in females ranged (in average values) within the limits of 3.8% to 23.5% annually (A.A. Vershinin).

Estrus in fur-farm sables extends from 15 June to 15 August (Starkov, 1940; Kler, 1941): from 6–25 July, 68% of all females have come into estrus, and from 11–20 July—38%, the mean date lies within 16–20 July (157 cases of 789). The earliest cases are twice as frequent as late ones. In nature, spermatogenesis was histologically established for the period from 11 VI to 29 VII (Raevskii, 1947). In August, sexual activity is suppressed. Estrus extends for 1–3 days with repeated mating, each of which continues from 30–40 min to 2h each. After a pause of 1–10, and up to 20 days, estrus is repeated. Full sexual quiescence in sable extends from the end of August to February (Kler, 1941). During this time, the development of the embryos, which are in the trophoblast stage, almost stops (latent period).

At the end of February-beginning of March, following phenomena very similar to those in the esterus period (up to vaginal cornification), the placentation [implantation] of the embryos takes place. Their subsequent development proceeds rapidly for 27–28 days (Kler, 1941). The phenomena of the so-called false heat are connected with the period of placentation. The reasons for this are not yet clear.

General duration of pregnancy is determined as 273–275 (Starkov, 1947) on 245–298 days (Kler, 1941); this variation is related to the variation in length of the latent period. The average duration of pregnancy is 273 days. The duration of the latent period of pregnancy in sable is determined to a minor extent by two factors: response to [passage of] time and the light factor—change in length of daylight. The artificial lengthening of the latter caused shortening of the latent period in 50% of experimental females (Belyaev, 1950; Belyaev, Perel'dik and Portnova, 1951).

Parturition takes place from 25 March-3 May, 83% of the cases occurring in a period of 20 days (9-27 April), and 50%—in 10 days (11-20 April: Kler, 1941).

The number of young in the litter is very tightly linked to the degree of favorableness of external environment (nutrition in particular); in Siberia [M. zibellina] and North America [M. americana), it varies from 1 to 7. In the Pushkin state fur farm, the average number of young in a litter equals 3 (Starkov, 1947); in the Moscow Zoo, it averages 2.8 (1.5)*. Sable in nature were determined to have an average litter size of 2.5 (Kosmakov, 1936); 546 in Barguzin sable, with the calculation of mortality before the beginning of harvest—0.7 (Z.F. Svatosh); in Kondo-Sos'vinsk sable—3.5 (Raevskii, 1947—30 cases); in sable of the northern Urals—3.0 (2-4) (Belousov, 1914); in the Eastern Sayan—3.0 (1-4) (Solov'ev, 1921); in Kamchatka—3.0 (2-4); on Bol'shoi Shantar Island—2.0 (2-4) (Dul'keit, 1929); in the Koryaksk range—3-6 (Sokol'nikov, 1927); in Shitkinsk region of Irkutsk oblast—3.3 (Timofeev, 1951). The average fertility of Barguzin sable on farms was determined as 0.92 and of Amur sable—1.76.

The potential fertility of sable, determined by the number of corpora lutea (without calculating embryonic mortality), is variable. In individual geographical populations, the average number of corpora lutea ranged from 2.3 (Barguzin and Gornoaltaisk sables) to 4.0 (Ivdel'skii region, Sverdlovsk oblast) and even to 5.0 (Tyumen oblast, 1952/53) (Zaleker, 1953, 1955, 1959; Baevskii, 1956). The average number of corpora lutea changes annually depending on the general stability of sable food; thus in the region of Barguzin preserve, with little food, the average number of corpora lutea was 2.3 (1952), and with an increase in food (1953),

^{*}Meaning of number in parentheses not clear-Sci. Ed.

it increased to 3.2 (Baevskii, 1956). In the Ivdel'sk region, in 1951/52 this indicator was 4.0 and in 1952/53—4.5; in Tyumen oblast—3.1 and 5.0 respectively (Zaleker, 1959).

Variations in the average number of corpora lutea with age were also noted in sables. In young female Barguzin sable in 1952. it was 2.7 and in 1953-2.3; in adult females in 1952-3.0, and in 1953—3.4: in old females—2.7 and 4.0 respectively (Baevskii, 1956). In Kamchatka, over 10 years (1952-1962), pregnant females among the second-year females had an average of 3.9 corpora lutea per female, and in all females of this age-1.08: among third-year pregnant females-4.01 and 1.86; and among older females—4.38 and 2.71 respectively. In very old females, 3 corpora lutea were found in pregnant females and the average number of corpora lutea in all very old females was 0.6. For the entire period, the average number of corpora lutea per pregnant female was 3.96, from 1 to 9. Calculating all females, the average number of corpora lutea was found to be only 1.93 (0.51-3.08). In second-year females, corpora lutea were (from a total of 1033) 21%; in third-year females—30%; and in older females—49%. Females 2-7-year old constituting 22% (on average) of the population, give 50% of the potential offspring, but the second half by older females, which constitute only 11%; i.e., the latter are potentially more (by 2 times) fertile. A definite dependence was established of potential fertility on the nutritional level of the female, its weight, and helminth infections (A.A. Vershinin).

Data on real fertility of sables in nature are extremely inadequate for introducing corrections to potential fertility; however,
it is clear that with different age composition of the sample
populations, the results will be different. Investigations in recent
years have shown that in martens with a latent period in pregnancy
[delayed implantation], ovulation takes place periodically before
placentation of the embryos in pregnant females. Although these
ova are not fertilized, the number of corpora lutea increases (Neal
and Harrison, 1958). Probably, this is also the case in sable and in
pine marten. Apparently, the number of corpora lutea may only be
considered an indirect indicator of the potential fertility, since it
may exceed the number of embryos even discounting embryonic
mortality.

Growth, development, and molt. Young sables are born help-less, blind, and with membrane-covered ear openings. At that time, they are covered with sparse light-gray down.

The average weight of newborn sables is about 30 g with body length of 11 to 12 cm (Starkov, 1947). A single pup may attain 34 g, while in large litters, it is reduced to 25 g. Sable cubs of larger races have a weight up to 32.8 g (with body length 11.9 cm).

The auditory orifices open on the 23rd-24th day; eyes—on the 30th-36th day (Starkov, 1947). Incisors erupt on the 38th day, and the replacement of milk teeth by permanent ones begins at the age of 3.5 months.

Sable cubs start to leave the nest at the age of 45 days. Lactation ends when cubs have attained 2 months of age. The utilization of animal food begins somewhat earlier—at the age of 50–52 days (Manteifel', 1934).

At one month of age the sable cub attains a weight of 260 g, at two months—600 g (Starkov, 1947). By July (the breeding period of the parents), they already weigh about 800 g with a body length of 39–40 cm, nearly attaining the dimensions of adult sables. With the transition to independent feeding, the growth of sables noticeably increases.

Among 195 newborn sable cubs, 49.2% were males and females—50.8%. Investigation of 1139 individuals from 1918–1930 showed that 56% were males and females—44% (Belyshev, 1950). According to other data (2,492), males in the population constituted 54.4%, and females—42.6%. Differences have been observed by regions (Nadeev and Timofeev, 1955). In Kamchatka, during 1939–1962, 3,967 individuals were investigated—52.9% males were found, females—47.1%. In the same place, according to track counts, from 1950–1958, 54.2% males were found and females—45.8% (A.A. Vershinin). In both cases it is possible that the percentage of males may be overestimated, in the first instance caused by selection for harvest, and in the second instance, caused by greater activity of males.

In the sable, there is a spring and an autumn molt.

Enemies, diseases, parasites, mortality, and competitors. The sables have few enemies among other animals. In this respect, young sables are exposed to the greater danger. The white-tailed sea eagle, eagle owl, goshawk, yellow-throated marten, wolverine and red fox are revealed to be enemies of young sables by factual observations. In all events, direct predation on sables cannot be considered as a factor affecting population numbers.

In nature, epizootic diseases of sable are undoubtedly present, but this question has been poorly studied. A die-off among sables

was observed in the West Siberian lowland (Raevskii, 1947), in Kamchatka (Averin, 1948), the Far East and other regions. It was also noted locally in the 60's because conditions of overpopulation were favorable for the development of epizootics. Among diseases that have been established are encephalitis, coccidiosis and skin fungal diseases.

In the sables, 14 helminthic species have been noted (Petrov, 1941). However, their pathogenicity is, in the majority of cases, unknown.

Mortality of sables is quite significant. Its magnitude is determined by many causes. First of all, the mortality of the population and its age composition depend on the intensity of exploitation and the degree of suitability of environmental conditions for the species. The magnitude of juvenile mortality (to one year) is very considerable. Under the severe conditions of the Koryaksk range (Sokol'nikov, 1927) and Bol'shoi Shantar Island (Dul'keit, 1929), the percentage of mortality during the first year of life was determined to be from 76.7 to 83.4. Just embryonic mortality lies within 8-31% (Baevskii, 1956, 1957; Belyaev and Utkin, 1960).

In the absence of exploitation, the Kondosos'vinsk sable population age groups were of the following: up to one year—42.6%; 1-2 years—28.5%; 2-3 years—23.8%; above 3 years—4.7%. Thus, in spite of entirely favorable ecological conditions, the intensity of the mortality rate of the population here was considerable and the average age is not high (P.B. Yurgenson). In Barguzin sables, the ratio of age groups observed was: young males—37%, moderate age-37%; old-26%; females were 59.4%, 31.2% and 9.4% respectively (Favorskii, 1935). Mortality among females was found to be significantly higher than that among males.

In 1952, in the commercial harvest on the territory of Barguzin 548 preserve, young females constituted 33%, adults-50% and old,-16%. In the following year, young [females] were 49.2%, adults— 42%, and old—6.8%. This appeared to be the result of intensive harvesting. In that same year, in an area where commercial harvesting had long been intensive, the percentage of young was 60.7%, of adults-39.3% and old females did not appear at all (Baevskii, 1956). These circumstances make it possible to estimate the intensity of exploitation through the age composition (Table 53; Nadeev and Timofeev, 1955).

From all these data it is evident that the size of annual growth in local sable populations may range from 10.5 to 30-40%. In the

Table 53. Changes in age composition of separate sable populations in different regions (630 individuals)

Age group	Vitim	Angara	Sayans	Kuzbass	Altai	Average
Less than 1 year	17.6%	32.0%	25.1%	14.5%	10.5%	28.5%
About 2 years	30.9	20.8	25.1	21.5	12.5	27.1
Older than 2 years	26.7	18.2	24.3	17.2	14.6	21.3
Particularly old	24.8	29.0	24.5	47.0	62.4	23.1
Examples studied	165	131	187	98	49	630

Shitkinsk region of Irkutsk oblast (Nadeev and Timofeev, 1955), during 5 years the percentage of yearling sables changed from 23.8 to 36.8% (average; 31.6%). In northwestern Yakutiya, yearlings comprised 1/3 of the population, and in the Oleneksk region (1950/51), 37% (Tavrovskii, 1958).

Age analysis of 1762 sable skulls from Kamchatka (collected 1945–1962) gave the following results (Table 54).

The decrease in the percent of young females is explained by their great utilization; there is information about the increased mortality among females from helminths (Kondrat'ev, 1957). During 1952–1962, the average percent of the juveniles in the population was 26.7%. This average changed annually for a series of years in the following manner (A.A. Vershinin):

%	%
1952/53—61.5	1957/58—14.3
1953/54—14.9	1958/59—81.5
1954/55—51.9	1959/60—43.7
1955/56—41.2	1960/61—15.0
1956/57—28.6	1961/62—50.5

For 10 years, the average percent constituted 40.3 (14.3–81.5%).

In Kamchatka, for the same decade the size of the potential increase was obtained based on the percentage of adult females

Table 54. Age composition of Kamchatka sables from 1945-1962

Age	Total	Males	Females
Juveniles	27.3%	21.5%	23.0%
18-22 months	22.1	19.8	24.3
In the 3rd year	19.4	19.3	19.5
Older ages	31.2	39.4	23.5

and the average number of corpora lutea (A.A. Vershinin). It is given in comparison with the percent of juveniles captured during those years (Table 55).

From this table may be seen sharp fluctuations in the average number of corpora lutea in females and hence potential fertility. However, in a series of cases (1952/53, 1958/59, 1959/60), the two latter figures are contradictory, explainable only as random selection of harvested animals as regards their age (A.A. Vershinin). In Kamchatka, 32.5% die during the embryonic and early postembryonic periods, and in the unfavorable years—50% of the potential increase. These figures are, apparently, lower than the actual size of population growth.

Animals consuming nut pine "nutlets" and carnivores feeding on mouse-like rodents may be referenced as the sable's competitors. However, few of them are of substantive significance; among the consumers of nut pine "nutlets" are the Siberian chipmunk and brown bear, as well as forest voles [Clethrionomys] which, however, themselves serve as food for sables. Nutcracker plays a positive role; on account of the making of its stock of nut pine "nutlets" on which the sable feeds in the snowy period of the year. Ermine, Siberian weasel, fox and other predaceous birds and animals of the taiga are considered competitors of sable in hunting mouse-like rodents. Siberian weasel, ermine and weasel are themselves actively pursued by sable. In areas where sable settle, the Siberian weasel disappears and is displaced into habitats less suitable for the sable (Shaposhnikov, 1956).

Table 55. Potential growth of sable in Kamchatka from 1952-1962

Years	Adult females, %	Average number of corpora lutea	Potential growth.	Juveniles in the harvest, %
1952/53	30.0	1.36	40.8	61.5
1953/54	43.5	0.84	36.6	14.6
1954/55	32.5	2.46	80.0	51.9
1955/56	27.4	1.80	48.5	41.2
1956/57	36.0	0.79	28.5	28.6
1957/58	43.5	3.08	134.0	14.3
1958/59	22.7	2.01	45.6	81.5
1959/60	30.4	0.51	15.5	43.7
1960/61	41.3	2.34	96.6	15.0
1961/62	25.3	2.70	68.4	50.5
Average	33.0	1.86	61.3	40.3

Population dynamics. Changes in their numbers is a characteristic of sables. Changes brought about by deep reconstruction of natural landscapes as a result of human activity are irreversible: the disappearance of coniferous taiga and the formation of the so-called cultural landscape, within the limits of which sable usually do not survive.

To those powerful factors influencing sable numbers, are also applied taiga fires and the hunting harvest. Diseases and starvation are less significant, since contact between sables in the populations is small and the sable is polyphagous, it suffers from food scarcity infrequently, and not everywhere. In cases when its density increases, the possibility of contact grows, and serious epizootics begin to appear among sables. Where human activity is excluded or weak (preserves), fluctuations in sable number are insignificant and are determined in combination with and as a consequence of, in some seasons, an accumulation of favorable or unfavorable environmental factors. In American marten, a certain cyclicity was observed in fluctuations of their numbers. Years of high number are repeated, on average, every 10 years, with deviations in the range of 9–11 years.

In Kamchatka, voles are of decisive importance as sable food (see above). Their mass reproduction there has a three-year cycle; *i.e.* similar to the so-called "Scandinavian cycle." As noted above, the level of fertility depends on the age structure of the population, caused by lower fertility of young females. With intensive reproduction when the main food is plentiful, the sable population attains a younger average age and therefore, in the following year, breeding intensivity is reduced. In the third year, the age structure becomes even less favorable for productivity of the population, and it falls to minimal increase. In the fourth year, the relative proportion* of the oldest age group increases, and the population growth again increases. Thus, the numerical dynamics of the population is determined by the availability of the main food: 1) environmental factors which determine changes in abundance of voles, and 2) by changes in population structure which change the level of fertility.

In those parts of the range where a considerable variety of alternate foods are present and the sable does not depend on the abundance of 1–2 foods (usually interrelated, for example, voles and nut pine "nutlets"), its numbers are subjected to smoother

^{*}In Russian original, literally specific weight-Sci. Ed.

fluctuations, depending on a combination of different factors and the cycle approaches 9–11-year interval. If, in Kamchatka, the numerical fluctuation attains an interval of 6 [years], in such regions with a prolonged cycle, it is 2–3 times lower; *i.e.* the population is more stable.

In the Glacier National Park (Montana, USA), the process of numerical change in concrete local populations in an area of 1.554 ha was studied by means of tagging and recapturing animals (1952-54). At the end of the summer of 1953, population growth was observed. After that, from September 1953 to December 1954, of 27 resident sables, nine were killed (30%). All the progeny of 1954 also migrated beyond the boundaries of the experimental territory. Density fell from 17.6 to 7.0 per 1000 ha; i.e. by 2-4 times. Five females died (18.5% of the population). Decline in the weight of trapped females was noted, and dead animals showed signs of emaciation and shock disease (Selve's syndrome). There was first overpopulation and exhaustion of food resources owing to reduction in numbers of the principal food—mouse-like rodents. Predominant mortality of females was explained by increased loss of energy (estrus, pregnancy, parturition, lactation) due to insufficient food. Moreover, in those places where females fed, their litters fed with them, and this accelerated the exhaustion of food stocks (Newby and Hawley, 1954; Hawley, 1957).

Field characteristics. Under natural conditions, most often only traces of sable activity must be dealt with. The animal itself may be met with rarely and accidentally; it is easier to succeed with the help of a good laika dog. The sable, driven up a tree, somewhat resembles a small cat, but differs in its fluffier fur, small sharp muzzle and relatively short fluffy tail. It is very similar to the pine marten, but usually may be distinguished by the lighter color of the head and somewhat shorter tail. The male can be easily differentiated from the female by its larger dimensions and muscular, burly shape: the females are thinner and more elegant. Tracks of sable are very rarely found in the snow-free period of the year, in the form of single prints. One may often find sable scat on taiga paths, on stumps and fallen logs. It is sausage-like in form with blunt ends, about 1.5 cm in diameter, and a length of about 6-7.5 cm. In it are usually found hair and small bones of voles, shells of nut pine "nutlets", fruit and insect remains. The scat gives off a musky odor.

Footprints of sable are broad, and disproportionately large compared to the animal's body size. The large footprints of a sable track are often not differentiated from those of red fox. The feet of sable are not held in a clump, distinguishing them from red fox. In a clearly printed sable track, the claws are not obvious; foot pads are not always visible, but are more frequently seen in summer. On packed snow, the average dimensions of the prints are equal to 4×6.5 cm (from 5×7 to 6×10 cm). Doubled prints of front and hind feet are usually large—from 5×9 to 8×15 cm. In large leaps on soft snow the prints of both feet are united in one depression of dimensions 10×25 cm. On packed snow, sable tracks form depressions 3-5 cm, and on soft snow—10-15 cm. In addition to paired prints, especially on packed snow, sable often trot. Then, the arrangement of the tracks is very similar to those of hare. Sable walks "cleanly" without leaving drag marks.

In the Siberian taiga, tracks of sable are similar only to the tracks of Siberian weasel, but only inexperienced hunters might confuse them. The tracks of the Siberian weasel are not located parallel to each other, as in sable, but somewhat overlap each other at the heels; this is less marked in the tracks of pine marten and *kidas*. When jumping from a tree, the pine marten does not leave the tail print on the snow, but the sable does. Passing under the crown of a tree, the sable greatly shortens its leaps, but the pine marten continues walking regularly. Moreover, sable never stays twice in one shelter, while the *kidas* does; sable go about widely under the snow completely covered with it. Pine marten and *kidas* can sit it out under the snow to the very last extreme (Raevskii, 1947; Yurgenson, 1948).

In the Urals, after a snowfall, sable begins to move after 2–3 days, when the snow has settled and when the animal sinks in not more than 3–5 cm.

Usually, the sable does not run the whole day with one gait. The length of the leap depends upon snow density. In soft snow, leaps are shorter and the sable places its feet more widely. In soft snow, length of the leap does not exceed 30 cm; in dense snow—45–75 cm. Separate large leaps reach 2 m; such leaps do not occur in more than 2–3 successive jumps. The average length of a leap in the montane taiga of the northern Urals is equal to 40–45 cm, ranging from 70 to 80 cm (Kondratov, 1953).

In the taiga of the eastern Sayan, the length of sable leaps ranges from 40 to 80 cm. The width of the paired tracks usually ranges from 9 to 14 cm and that of one track—from 4.0 to 5.5 cm.

The sable foot sinks into the snow for 5–10 cm. Weight loading is equal to 12–14 g per 1 cm² (Dul'keit, 1957), in the northern Urals, even with a body weight of 1200 g, it ranges from 9.5 to 11.7 g (Kondratov, 1953). The average length of a leap in a male Sayan sable in soft snow is equal to 51.5 cm, of a female—37.5 cm; the paired prints of a track in females average 11.0 cm (9.4–11.9), of a male—13.3 cm (12.0–14.6).

In the most typical gait, which make paired prints, the posterior pair of feet lie in the prints of the anterior pair. One of the feet is usually displaced forward, and there is no regular alternation of the right and left feet. A triple print, in which one of the posterior feet does not lie in the print of the anterior foot, is infrequently observed and is usually noticed when there is little snow, when the sable feels firm support. It rarely places all of its feet separately (as in red fox). The speed of movement of sable is 7–8 km/hour, and in one minute it makes 200 leaps, of 60–70 cm each. Walking, the sable ambushes its prey; it steps, it listens, considers etc.

Individual sables can easily be distinguished from one another by the length of leap, the width of feet placement and depth of sinking into the snow, since these values depend on the weight and size of the sable. In order to travel 1 km, the male makes on average 1900 leaps, and the female—2400, but in soft snow—2500 and 3300 respectively. Consequently for the same distance, the female requires more energy and therefore, its daily trail is always shorter. The length of the trail is shortened with an accumulation of soft snow, when leap length decreases and sinking of the animal into the snow increases (Dul'keit, 1957) (P.Yu.).

Practical Significance

The sable is the most valuable fur-bearing animal in the USSR although, as a commodity, the quality of the skins is not of the same value in different geographical regions and even in the same locality (see above, "Description" section).

Excessive, often rapacious, exploitation of sable in the past exhausted the stocks of this animal. Its range was also strongly reduced. In order to restore their number and range, a series of preserves were organized, their exploitation was prohibited for a long time and broad encompassing measures for artificial reintroduction of sable were undertaken in regions where it had been

552

extirpated. As a result, the number of sable and the area inhabited by it increased considerably. The number of sable attained such heights that in some parts of the range a surplus of sable developed with a series of negative consequences. Captive breeding of sables developed widely and attained significant success.

At the present time, within the boundaries of the USSR, about 33% of the sables caught each year come from Krasnoyarsk Territory, about 20%—from Irkutsk district, about 16%—from Khabarovsk Territory. With all of this, at the present time, not all the areas in the Siberian taiga suitable for their occupation have been taken up by sables. At the present time, the tendency is towards increase in the number of light-colored sables. Therefore, there stands the problem of devaluation in the direction of natural selection of sable with the entire improvement in the quality of the skins on a large scale.

A very important measure for management of the sable population is to determine correctly a guide to the amount of utilization (the percentage of the admissible catch) and maintain it. For a very high density, the catch should be accelerated. The example of Kamchatka can illustrate this situation: a catch of 7.5–8.0 thousand sables in a season does not lead to a decrease in their number, but a catch of even 8.5–9.0 gives this effect. In Kamchatka, it is admissible to take 27% of the autumn pre-harvest number (A.A. Vershinin). In other places—25% and 30% (Baturin, 1930; Vershinin and Dolgorukov, 1947). It is important to change the size of the catch in relation to the condition of their numbers: for Kamchatka—the limits are between 15% to 65% (A.A. Vershinin).

The main methods of sable capture are hunting with guns, with the aid of *laika* dogs, harvest by trapping, and the application of baits. Different wooden deadfalls, snares, and live-traps of the box type are also used. The hunting of sable by baits helps to obtain them alive, which is important for the purpose of reintroduction, selection, banding, etc. The sable harvest is regulated by the issuance of special licences.

Measures for the effective protection of sable should include: 1) strict maintenance of rules and norms of licenced harvest; 2) prohibition of selective destruction (which is possible by baits of high quality sables through establishing "average" prices for each fur type. Otherwise, the hunter, having a sable hunting licence, will always try to take only sables of the highest sort, thus increasing the low quality sables in nature; 3) banning overharvest in core habitat (as regards quantity and quality) throughout the enitre range, as well as other measures.

It is desirable to prohibit periodically the harvest, even with licences, after seasons unfavorable for sables (famine, forest fires, diseases and others) and to organise supplemental feeding in the winters of famine. It is also necessary to put into practice a harvest with planned selection of sables in nature through issuance of special licences for trapping and shooting of only the lowest quality sables ("mekhovaya" and in some cases, "vorotovaya").

The greatest efforts should be directed towards the develop-553 ment of excess populations in unharvested and poorly harvested regions, and towards the prohibition of overharvesting in areas lying close to the inhabited areas, and those more convenient and easier to develop (P.Yu.).

FOREST MARTEN²⁶*

Martes (Martes) martes Linnaeus, 1758

- 1758. Mustela martes. Linnaeus. Syst. Nat. Ed. X, 1, p. 46. Upsala, southern Sweden.
- 1816. *Mustela sylvestris*. Oken. Lehrb. Natgesch., 2, p. 1029. Substitute for *martes*.
- 1820. Mustela sylvatica. Nilsson. Scand. Fauna. Dagg. Djur., 1, p. 41. Renaming of martes.
- 1827. Martes vulgaris. Griffith. Cuvier's Anim. Kingd., 5, p. 123. Renaming of martes.
- 1865. Martes abietum. Gray. Proc. Zool. Soc. London, p. 104.
- 1926. Martes martes lorenzi. Ognev. Uchen. Zap. Sev.-Kavk. Inst. Kraevedeniya, 1, p. 47. Storozhevaya, Kuban district.
- 1926. Martes martes ruthena. Ognev. Ibidem, p. 49. Dmitrovsk, Moscow province.
- 1941. M.(artes) m.(artes) ruthena borealis. Kusnetzov. Tr. Mosk. Zootekhn. in-ta, 1, p. 126. Shenkursk region, Arkhangel'sk district. Nomen praeoccupatum—Mustela flavigula borealis Radde, 1862.

²⁶Also called "zheltodushka" [yellow-breasted] and "kunitsa myagkaya" [smooth marten] by furriers.

^{*} literally, "forest marten"—Sci. Ed.

- 1941. Martes martes uralensis. Kusnetzov. Ibidem, p. 126. Vic. Miass, southern Urals.
- 1947. Martes martes sabaneevi. Jurgenson. (Yurgenson). Tr. Pechoro-Ilychsk. zapov., 5, p. 179. Pechoro-Ilychsk preserve, upper Pechora (V.H.).

Diagnosis

Tail length with terminal hairs more than half that of body. Color monotone, sharply outlined patch of various forms on throat and chest, usually varying intensities of yellow color, sometimes white or almost white, and as a rule, not forming two strips extending backwards to base of forelegs. Head not lighter than back. Bony auditory bulla relatively shorter and more widely separated than in sable. Inner half of upper molar considerably larger than outer (V.H.).

Description²⁷

In its general appearance, the pine marten in winter pelage is very similar to the sable, but looks somewhat larger, coarser and longer tailed. Tail length with terminal hairs is more than half the body length—in the animal "in the flesh", the tail extends behind the stretched hind legs usually for more than a quarter of its length. In contrast to the sable, the terminal hairs of the tail do not form a blunt, but a tapering tail tip. This tip is sometimes strongly elongated (majority of cases), typical of marten, sometimes tapering to an obtuse cone-shape, and sometimes (minority of cases) has the blunt "sable-like" form (Urals; Pavlinin, 1959). Length of the terminal hairs, in typical cases may reach 100 mm. Foot pads are less furry, and appear to be less broad. Ears, in sable, are also broad at the base, but shorter and more rounded at the tips, from which 554 the whole head looks relatively smaller than in the sable, and more elongated, with a longer facial portion. Feet are covered below with dense and quite coarse hairs, somewhat less developed, however, than in sable, the sole and digital cushions are completely covered with hairs, but the ends of the claws protrude from the fur.

²⁷Some additional data, characterizing the pine marten, are given in the description of the stone marten.

In summer coat, the marten is distinguished from the sable by the same characteristics, but appears even coarser and more long-tailed, with less broad feet and not so big-eared. In its manner of standing and moving the marten is entirely similar to sable, but differs considerably from the stone marten, which mostly "crawls" and rarely proceeds by jumping. This is connected, in part, by the height of the animal at its shoulders: in the pine marten, this constitutes about 15 cm (Schmidt, 1943) and more than in the stone marten.



Fig. 208. Pine marten, or zheltodushka [yellow-breast], Martes (Martes) martes L. Sketch by A.N. Komarov.

The pelage of marten is similar in structure to that of sable, but is somewhat rougher and less dense and fluffy. Nevertheless, it is one of the smoothest and most delicate furs and one of the most valuable. Compared to winter, the summer fur is short, coarse and relatively thin. In summer there are 4–5 underhairs for each guard hair. Length of the guard hairs is 23–27 mm, with a thickness of 100–150 microns, length of underfur is 11–12 mm, with thickness of 15–16 microns. The corresponding figures for the winter fur: guard hair, 36–38 mm and 75–90 microns, and underfur, 22–22.5 mm and 14.5–15 microns (Pavlova, 1951). Thus, the winter hairs although longer, are relatively much thinner. In the summer coat of marten, the sole and finger cushions as well as the claws are easily seen. In winter, the tail is much fluffier than in summer and with longer terminal hairs.

The general color of the winter fur is brownish-reddish or reddish-chestnut with a strong straw-gray wash, depending upon the general tone of the underfur. This wash is particularly developed on the sides, where the underfur is not so completely covered by dark guard hairs, as on the back. The back is darker than the sides, as are also the middle of the abdomen and the inguinal region, but lighter than the middle of the back. The top of the head is dark, no lighter than the back. The upper edges of the ears and their inner sides are whitish-straw, the reverse side of the ear dark brownish. The feet are blacker and darker brown than the back. The basal part of the tail is colored like the back, and its tip is darker.

A light patch with sharp outlines is located on the throat and the lower surface of the neck. In a typical case, the patch occupies the throat and the lower surface of the neck, without extending to its sides but projecting backwards as an extension onto the chest between the forelegs. Its borders are usually sharply outlined, but they are sometimes diluted on the neck. In general, the form and dimensions of the patch are variable. Usually it develops in a more or less typical shape, but sometimes is rounded (backward extension is absent) or greatly reduced. In some instances, it is divided into separate parts and, rarely, may be reduced into some small white marks, or disappear completely. Sometimes there is a dark spot in the middle of the light field. Sometimes, on the contrary, the patch is enlarged and covers not only the throat, but the anterior part of the chest and the upper part of the forelimbs. In some

cases, though it is very rare, there are two extensions towards forelimbs, as in the stone marten. As an exception, the posterior extension of the patch may, on passing between the forelimbs, extend quite far along the abdomen. There are some geographical tendencies in changes in size (not form) of patch (see below).

Though the general color type is retained, its tone and intensity undergo considerable individual fluctuation. One may distinguish four main color types of martens which are accepted in the fur industry (furriers terminology).

Dark blue-fur dark-chestnut without reddish tints, underfur bluish-gray at the base and light-gray at the tip.

Blue—pelage lighter, chestnut colored, underfur grav.

Dark sandy—fur brownish ("dark-sandy") with reddish tints. more distinct on the sides. Underfur gray at base and light-sandy color at hair tips.

Sandy—pelage light-brownish ("sandy") with light-yellow tint. Underfur gray at base and yellowish at the tip (Kuznetsov, 1952).

Sometimes, skins have "grizzled" highlights-scattered white guard hairs; however, these grizzled ones are much less developed than in sable and are rarely encountered.

Under various conditions, "dark blue" martens are considered the most valuable. The same tendencies are also noticeable in geographic variations in marten fur, however, they are quite weak and much weaker than in sable and the phenomenon of parallelism itself is less marked.

The color of the throat patch is, as a rule, yellow of varying intensity, changing from slightly ocherous to bright intensive ocherous, almost orange. Near-white and white patches occur. There 556 are several geographic tendencies in the intensity of patch color.

Among martens of the European part of the USSR, the most southern (Kuban) martens have the brightest orange patch; northward, intensity of its color decreases, and it lightens. The same picture is also observed in the Urals—from the north to the southern extreme of the range. Along with this, the general size of the patch changes with some regularity. In the Urals, the number of martens with a large throat patch increases from north to south. In Bashkiriya, martens with small patches are relatively very few. In a few instances (more often in the northern Urals), the throat patch may completely disappear. Such individuals in several sections of the range in the Urals constitute 1-3.2%, sometimes even to 7.1%

(Kuznetsov, 1952; Pavlinin, 1959). White or near-white patches are sometimes found, or having a form, similar to the form typical for stone marten. Such individuals are very rare, and only one among several hundreds are met with—in the Urals, one among 900 (Pavlinin, 1959)²⁸.

The density, luxuriance and fineness of the pelage i.e. fur quality, undergo marked geographical changes which are, however, much less than in sable (see section "Geographic variation"). Individual and geographic variation in marten are on the whole, much less than in sable. Geographical localization of types of individual variation so characteristic for sable is absent in marten, or it is more weakly manifested.

Summer fur is characterized by yellowish-brown color of the underfur and dark-brown color of the guard hairs. The relatively strong development of the guard hairs, with dark underfur, confers a general dark-brown color to the animal, which is much darker than in winter. The tail, particularly its tip, and the feet are darker than the trunk—blackish-brown. The throat patch is usually brighter than that in winter marten. Individual variation in color of summer fur of martens is much less than in winter.

There are no sexual and age differences in color and character of the pelage (fur quality). Young in the first autumn put on a coat that is not distinguishable from the winter coat of adults.

The skull of pine marten is very similar to the skull of sable. It differs from it by the not so elongated brain case and by its shorter and more widely separated bony auditory bullae—the distance between them in the middle part of their length is more than half the length of the bulla, measured from its anterior edge to the posterior point of the paroccipital process. The mastoid processes slightly extend outwards behind the edge of the auditory openings. The interpterygoid cavity is somewhat wider than in sable. The dental formula is as in sable, but the inner blade of the upper molar is usually somewhat larger and the difference between the inner and outer blades is greater.

Sexual differences are expressed in the smaller general measurements of the female skull, the weaker development of

²⁸Particularly such individuals, apparently, were given as the reason for the appearance from time to time of confirmations about hybridization between the stone and pine martens, originating mainly from fanciers but penetrating later into scientific literature, which in actuality does not occur (see below, chapter on stone marten).

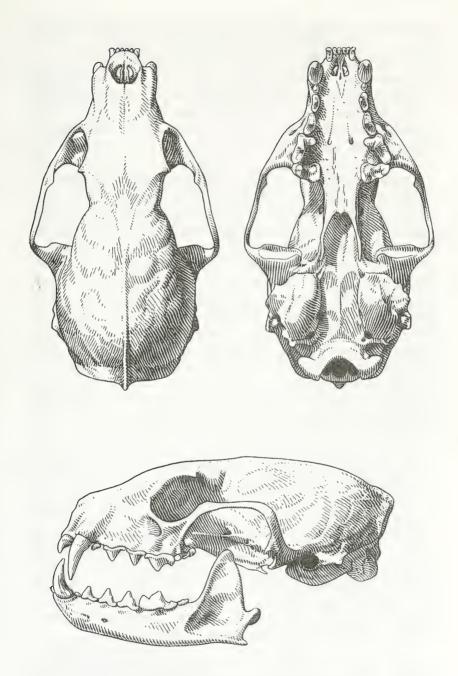


Fig. 209. Skull of pine marten, Martes (Martes) martes L.

protuberances, crests, etc., and on the whole, in the somewhat lighter structure of the skull. In the martens of Volga-Kama basin, the condylobasal length of the male skull is more than 78 mm and the zygomatic width is more than 45 mm; in females, correspondingly—less than 76 mm and less than 42 mm (Aspisov, 1959). Age changes in the skull are significant and, in general, correspond morphologically to those described for sable (age conformity is not established).

The skeleton of the tail is composed of 15–22 vertebrae, *i.e.* on average, several more than in sable; Caucasian martens have 18–21 caudal vertebrae; Pechora—17–20 (17—5%, 18—40%, 19—25%, 20—30%; Yurgenson, 1947). Male martens of the middle and southern Urals and Bashkiriya have 15–20 (n 100), with 15 found very rarely, 17 also; most often, individual variation lies within 16–20 or 18–20, 17.9–18.7 on average. In females (n 84) the number of caudal vertebrae is 16–20, with 16–17 often found, the average lying between 17.6–18.9 (Pavlinin, 1959). The clavicles, which are rudimentary in all species of the genus, are articulated neither with the sternum nor with the scapula and lie in the muscles; they are weakly curved, having their basal part shorter, the distal part longer, flattened, thinning distally and tapering at their ends; their length is about 13 mm.

Both projections at the distal end of the os penis unite with each other and form a closed ring. Only in young animals they are often separated, as in sable (Yurgenson, 1947).

In dimensions, the pine marten correspond more or less with sable, usually averaging somewhat less than the latter. Within the species, body length is 380–580 mm, tail length, 170–260 mm, length of hindfoot, 62–93 mm, and ear height, 40–45 mm.

Sexual differences in dimensions are quite marked (Table 56).

Average values in the different parts of the region mentioned differ in the following manner: body length of males—422–439; females, 387–405 mm; tail length of males, 195–207; females, 185–195 mm; hindfoot length of males, 81.5–85.8; females, 73.9–78.0 mm; ear height of males, 45–47; females, 44.5 mm; weight of males, 795–850 gm, females, 542–620 gm²⁹. Weight of the female skin constitutes 68.4% of the weight of the male skin.

²⁹Weight of carcass given without skin, *i.e.* it is actually somewhat larger. The weight of a freshly skinned hide in the same region comprised from 96 to 159 gm (Pavlinin, 1959). It is possible that some other measurements provided by the author (body length?), are also not standard, but are of the same type and give a representation of the relative dimensions of the different sexes.

Dimension Males, n Females, n Body length (mm) 93 405-473 102 365-420 Tail length (mm) 104 185-228 100 170-210 Hindfoot length (mm) 84 78-93 78 70-84 6 45-47 Ear height (mm) 4 43-46 Weight29 (gm) 59 670-1050 49 484---850

Table 56. Dimensions of male and female martens of the middle and southern Urals and Bashkiriya (from material of Pavlinin, 1959)

Condylobasal length of male skull, 72.1–88.0 mm; females, 71.1–83.0 mm; zygomatic width of males, 41.4–53.8 mm; females, 38.2–49.2 mm; skull height in males, 27.4–34.9 mm; females, 27.0–31.8 mm (from material of Kuznetsov, 1941). Weight is 580–1800 gm.

In adult martens (older than 2 years), length of the os penis is 38.9–45.7 mm, M 42.3 mm; weight, 0.20 to 0.35 gm, M 0.29 gm. In young, length is 35.1–38.3 mm, M 0.16 gm (Popov, 1943; Yurgenson, 1947; Aspisov, 1959). The preputial part of the male copulatory organ is short—about 26 mm long (Shtreili, 1932).

In martens of the Urals and Bashkiriya, length of the intestine of males is 157–245 cm, females, 140–197 cm; heart weight of males, 6.3–10.6 gm, females, 5.4–8.4 gm. The heart index is 8.5–9.2‰, but may be from 4.3 to 11.5. Weight of the liver of males is 18.3–46.9 gm, females, 14.5–35.2 gm. The percentage relative to the body weight constitutes 27.0–33.8% in different populations (Pavlinin, 1959)³⁰.

Kidas.³¹ In those places where sable and marten occur together and particularly in the Urals, in the Pri-Urals and beyond the Urals, hybrids are formed between them, known as *kidus* or *kidas*.

It is agreed that kidas are fertile, both between themselves and in back-crossing. Only experimentally (on farms) was there established a restriction on kidas fertility—females are fertile in back-crossing both with sable and with marten; in this combination, males were shown to be infertile. Fertility of kidas among

559

³⁰The given figures, some at least, were apparently taken from frozen carcasses and assigned to the weight of the body without hide. See the data on other internal features in the present work.

³¹There are very many reports on kidas and separate notes on it in the literature. Yurgenson (1947) discussed this question most completely on the basis of good material. The information provided here, if not attributed, was taken from this study.

themselves was not established. There were not, apparently, sufficiently extensive experiments of this kind.

This complex hybridization mentioned above leads to a situation that on one level individuals with more or less defined intermediate characteristics more similar to martens—"marten-like" type, and also those in which the sable features prevail ("mixed pasture sable" as they are referred to Pechora hunters), and finally, some which possess novelties of fur quality, proportions, dimensions (heterosis), etc. Certain individuals do not exhibit external features of hybridization and their actual nature can only be determined by special investigations (skull, skeleton).

Because of this heterogeneity of kidas populations, their characterization is extremely difficult and cannot be given in the form of a diagnostic key. "The range of individual variation (of kidas, V.H.) is extremely great. For almost every feature we may find deviations towards one of their original parental species up to complete identity, as well as intermediate characteristics. Finally, there are also localized and sharp modifications of deviation, as well as phenomena of innovation and heterosis. All these are encountered in multiple different combinations. Therefore, the identification of kidas is only possible on the basis of a combination of characteristics, or by simultaneous unification of features of both original species" (Yurgenson, 1947).

Externally, the typical *kidas* of the upper Pechora [river] are usually characterized by the whitish color of the head, as in sable, the tail, short as compared to marten, but longer than in sable, and by pelage that is usually dark or black in general color and denser, longer and more luxuriant than in marten. The fur, however, is coarser than in sable, with denser and thicker guard hairs, and without such a lustrous and silky appearance. In some cases, the fur closely corresponds to one or the other of the initial species, and its hybrid nature is revealed in other features (more often in length and fluffiness of the tail).

Particularly characteristic is the usually well demarcated, bright colored throat patch. In some cases, coarse fur occurs without the silky appearance and luster, with dense and long guard hairs differing from the fur of both initial species. In this case, the animals usually manifest particularly large size, a massive, rough appearance and a heavy angular head. Concerning the general color type in a series of *kidas* from the Pechoro-Ilych reserve, 54% have the

marten type and 46% the sable. Concerning tail length, 40% are closer to marten and 60% to sable.

Kidas of the same reserve are also of different size; on the average they are smaller than sable (which is larger than marten in the Pechora), but larger than marten. Individual animals are larger than the largest martens and are nearly of the same size as the largest sable.³² The dimensions of kidas (24 males, 10 females) are as follows: body length of males—390-M 452-485 mm, females—365-M 406-450 mm; tail length of males—170-M 187-240 mm, females—110-M167-180 mm; hind-foot length of males—75-M 86-98 mm, females—70-M 73-77 mm. Length of os penis 36.7-M 40.6-44.7 mm.

Weight of males 600–M 754–980 gm, females 410–M 551–680 gm. In relative length of tail, *kidas* occupies an intermediate position between sable and marten. In sable of all ages, this is equal to a mean ratio of 2.7 (females, 9) and 2.9 (males, 14); in marten, it is 2.0 both in females (213) and males (251); and in *kidas*, 2.5 (females 6) and 2.4 (males, 6) (Yazan, 1962).

Condylobasal length of skull 74.8–M 81.5–88.2 mm; zygomatic width 52.1–M 55.6–58.1 mm; skull height 36.1–M 38.5–42.8 mm (10 spec).

The structure of the os penis in the majority of cases (more than 90%) is that typical for marten (closed ring at the end).

Craniological features of *kidas* also delineate a very complicated picture. Thus, out of the 40 skull measurements of Pechora *kidas*, 35% have an intermediate characteristic between martens and sables. On average, 17.5% of measurements are similar to those of sable and 47.5% are like those of martens. For example, zygomatic width, length of nasal bones, width of cranium and others are sable-like; length of auditory capsule, postorbital constriction, skull height, etc. are marten-like.

The distribution of different upper molar structures among individuals is as follows: 41.6% of *kidas* have "sable-like" teeth, 41.6%—"marten-like" type, and 16.8%—intermediate characters.

 ³²According to other data (Yazan, 1962), kidas of Pechora-Ilych reserve (14) are larger than both martens (463), and sables (23) of the same place. The discrepancy in the data of Yurgenson (1947) is explained by the fact that the latter compared Pechora martens and kidas with Kondosos'vin, i.e. the Trans-Ural sables, which are larger than the Pechora. Absolute figures presented by Yazan (1962) could not be used because the means of obtaining them are not clear (fresh carcasses with fur, frozen carcasses with fur, or frozen skinned carcasses?).

A marten-like postorbital constriction is present in 8.3% of *kidas*, sable-like—33.3%, and transitional type—58.4%. It was noted that in individual *kidas* more features of one or the other species occur.

In practice, very multiform combinations are met with in kidases: os penis of the marten type, postorbital constriction and pelage of the sable type, tail as in pine marten; in craniological features, more sable characters, etc. Clear intermediate forms are sharply distinguished, such as light Ural sable with long marten-like tail.

In different places, evidently in connection with the correlation between initial species, the *kidas* population deviates more to one or the other side. At the sources of the Pechora, the marten type is more common, beyond the Ural, the sable type.

The percentage of kidas in the population may be very high—for example, on the Pechora: marten—58.8%, kidas—29.6% and sable—11.6% or 80%, 7%, 13% respectively. When marten and kidas only were hunted (sable was prohibited), at the sources of the Pechora river and along the Ilych, the ratio of marten to kidas in different places was 85 and 15%, 79 and 21%, 72 and 28% and even 65 and 35%³³ (V.H.).

Systematic Position

See sections on sable and stone marten.

Geographic Distribution

In Europe, western Siberia, Caucasus, Asia Minor and Iran.

Geographic Range in the Soviet Union

This constitutes about half of the species range. It is located in the western, and in part the southwestern, sections of the USSR. Within

³³After completion of the manuscript of this volume, the work of Pavlinin appeared ("Tobol'sk sable", Sverdlovsk, 1963), in which, contrary to the accepted idea, the existence of *kidas* is denied. According to the conviction of the author, individuals considered as hybrids are merely individual variants of sable or marten. Those general considerations that are reported in connection with the existence of these inter-specific hybrids (absorption and displacement of one species by the other, the formation of races of, hybrid origin, etc.) are also rejected.

At the same time, the author assumes that *kidas* in nature all "appear under exceptional conditions" (page 105), providing in substance the same reasons that other authors have argued for the appearance of *kidas*. This question requires further study.

561

the limits of our country, the range is divided into two parts— European-Siberian and Caucasian, which are completely separated from each other by steppes, but are united farther to the southwest.

The northern border of the range in the west starts on the Kola Peninsula, at the state frontier at the latitude of Kola, or a little to the north (the most northern point of occurrence in the USSR), and passes to the southeast along the forest edge (Pleske, 1886) extending towards the White Sea along the southeastern coast of the Kola Peninsula. Farther on, the border is formed by the White Sea coast, to which the range almost everywhere, extends except, apparently, to a section northwest of the Kuloi river mouth. On this part of the coast, the border crosses the lowermost Mezen' and Kuloi rivers (Zhitkov, 1904) eastward including the upper course of the Semzha (flows into Mezen' Gulf a little north of the Arctic circle) and passes through the southern part of the forest-tundra in the basins of the Peza (right tributary of the Mezen') and Tsil'ma (left tributary of the lower Pechora) rivers. East of the Pechora, the borderline passes approximately along 67° N. lat. (V.Ya. Parovshchikov).

Beyond this line long transgressions occur—the Kola Peninsula to Iokan'ga on the [White] Sea coast, 50 km from the forest border (Smirnov, 1901) and at Kiya station, on the western shore of the Kanin, approximately 200 km north of the place of permanent occurience at the mouth of the Semzha (V.Ya. Parovshchikov).

According to 30's data, the border of the range in the Urals and western Siberia inclusively took the following form. It crossed the Urals somewhere at the region of 65° N. lat. (Ognev, 1931; Adlerberg, 1935), and along the eastern slope of the Urals, turned abruptly to the south, not extending onto the plain, and not crossing to the east of the Sos'va river. Approximately, at 61° N. lat. the borderline sharply turned back to the east, and at the watershed of the Tapsyi (Sos'va basin) and Tavda (Pelym), passed onto the West Siberian plains. Passing eastward, it crossed the sources of the Konda river, ascending along the left tributary of the Ob'—the Endyr' river—and at about 62° N. lat. crossed the Ob' river. Beyond the Ob', the range occupied the region of the lower Nazym where it reached 62° N. lat.

Farther on, the border extended southward along the Irtysh river to 60° N. lat. and again sharply turned back to the east.

Following this parallel, in general, or a little farther to the north, it nearly reached the Ob' (Nizhne Vartovsk yurts at the mouth of the Vakh). From this place, the borderline directed itself southwards to Vasyugan at the mouth of the Nyurol'ka (Nyarel'ka) and, forming its southern border, it turned around towards the southwest to the sources of the Dem'yanka (Skalon and Raevskii, 1940). Thence, moving in the same direction, it crossed Irtysh and the lower Ishim and, proceeding a little northward to 56° N. lat., through Golyshmanov and Yalutorovska regions, it passed on to the Urals through Sysert' to Nyazepetrosvk. Thence, it directed itself southward to include the Ural [river] extending into its valley to reach Chkalov.

An isolated section of occurrence, analogous to those found in the European part of the USSR (see below), is located in the Sanarsk pine forest and in the steppe west of Troitsk (Shvarts, Pavlinin and Danilov, 1951).

Therefore, the range of the marten in Siberia itself forms a triangle, the apex of which is directed to the east. It has as its base the Urals between approximately 65° N. lat. and 56° N. lat., and nearly reaches the middle Ob'*.

Information at the beginning of the 50's (Laptev, 1956) show a range of larger dimensions. If for several places this change undoubtedly depends on more accurate determination of the actual situation, then, all the same, it must be considered to occur mainly because of the broadening of the range, which is connected with the general increase in marten numbers and their spread to the east. Along the left bank of the Ob', marten are observed in the Shuryshkar region, at approximately 66° N. lat., *i.e.*, only a bit more to the south than on the right bank of the Pechora. Apparently, at this latitude, it also crosses the Ural [mountains].

Farther, the border descends to the neighborhood of Berezov on the Ob' and, going eastward, encompasses the basin of the Kazym—the Khetu and Sorum rivers, the Trom-Yogan basin (Trom-Agan, right tributary of the Ob'), and the Vakh basin (Sabun and Korlika rivers in their upper reaches). The marten was also noted at Nizhne Vartovsk at the mouth of Vakh and on the Ob' at Lukashkin above the mouth of the Vakh. The range includes the basin of Bolshoi Pasol river—a tributary of the Ob', and the basin

*Not clear; the range as described and mapped does reach the middle Ob'; unless this is meant to refer to 1920-30 period (see Fig. 211)—Sci. Ed.

563

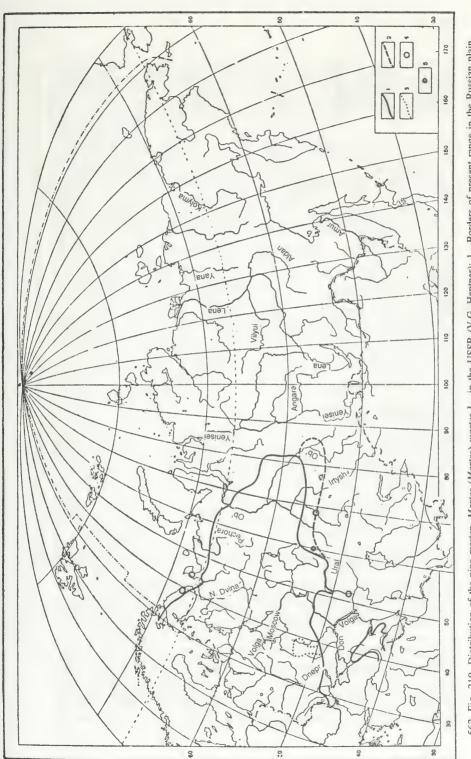
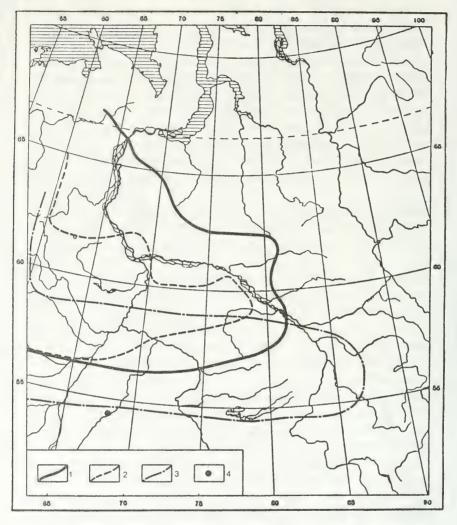


Fig. 210. Distribution of the pine marten, Martes (Martes) martes L., in the USSR (V.G. Hepmer): 1—Borders of present range in the Russian plain and the Caucasus; 2-Proposed border of the region of occurrence in the south of West Siberia in the XVII cent.; 3-The approximate outlines of the region where marten is absent; 4--Points of long-distance transgression of individual animals; 5-Isolated region of occurrence in Sanarsk pine forest (for details on Siberian part of range, see Figure 211). 562



563 Fig. 211. Borders of the distribution of pine marten, Martes (Martes) martes L. in western Siberia (V.G. Heptner): 1—Border at the beginning of the 50's of the XX cent.; 2—Same in the 20's and 30's of the XX cent.; 3—Proposed limits of the range in the XVII cent.; 4—Transgression south of Petropavlovsk.

of the Vasyugan. Thence, the border of the range passes to the Irtysh at the mouth of the Tara and is directed west, to the north of Lake Saltaim—a little north of 56° N. lat. Farther on, the border coincides with the [previous] description (for the distribution of marten in Siberia, see below).

There is poorly defined information concerning the appearance of (transient) pine martens far to the south in riparian forest tracts, along the Ishima around Yavlenka about 100 km above Petropavlovsk (Leninsk region of North Kazakhstan district; Sludskii, 1953).

The southern border of the range in the European part of the Union in the west covers the forest regions of central Moldavia on the Kodora (Kuznetsov, 1952). Crossing the Dnestr, it includes the Balty region (former Baltskii co.; Orney, 1931) and Sayransk forest (west of Pervomaisk), passing toward Dnepropetrovsk (Samarsk pine forest, the Samara river which flows into the Dnepr from the left: Yurgenson, 1932) and farther, to Izyum and to the mouth of the Oskol in Donets (former Izyumskii Co.; Ognev, 1931). From the mouth of the Oskol, the border extends to the Don, leaving it around Pavlovsk (Shipov forest) and thereafter, to the Khoper around Novokhopersk (Tellermanovsk grove; Ognev and Vorob'ev, 1923). Along the Khoper, the southern border of the range ascends northward, approximately to 52° (Turka), and thence goes eastward, reaching the Volga at Saratov or a little below (it occupies the forest-steppe on the left bank; El'pat'evskii, Larina and Golikova, 1950).

In the above-described segment of the southern border of the range, the marten extends into the forest-steppe zone, and its actual outlines are very complicated. The described line passes through the extreme southern localities, in part separate islands of forest massifs or along the southern extremities of the riparian steppe forests. Therefore, its [delineation] here is strongly schematized and basically of a conditional character.

In nature, the border line bends more or less northward in a number of places, over the unforested steppes of interfluves. Such is the picture between the Dnestr and Bug, the Bug and Dnepr, and between the Dnepr and Donets. The range border withdraws [to the north] particularly strongly in the areas between the Donets, the sources of the Oka, and the Don. Here, from the Izyum region, the border ascends sharply to the north, along the Oskol. Leaving the forestless regions of Maloyaroslavts, Liven and El'ets beyond the range, the border extends to Orel and then turns to the east, through Novosilya region (Ognev, 1931), and crosses the sources of the Don, and goes to Ranenburg (Tupov, 1925) or a little south, and then descends, as an extension, along the Tsna to Tambov.

From Tambov or from the sources of the Don, in an unclear way, it descends to Voronezh and then along the Don to Pavlovsk, reaching the previous line.

For all of that, marten distribution in the basin of the Don is extremely sporadic and is associated with the separate forest masses along the rivers or on watersheds. Thus, in the Voronezh district, marten was known from Voronezh preserve (Grafsk forestry allotment) and neighboring forest massifs, in the forests along the Bityug, and particularly around Bobrov and in the Khrenovsk forest (N. Severtsov, 1855; V.G. Heptner), around Novyi Kurlak and in several other places, in the Kamennaya Steppe (Dokuchaevsk Experimental station around Talovaya station), and in the Shipov forest near Pavlovsk (Ognev and Vorob'ev, 1923).

Beyond the Volga the border, apparently starting near the city of Engel's, goes northward along the floodplain of the Volga to the mouth of the Bolshoi Irgiz. From there, it passes along flooded forests of this river eastward nearly to Pugachev, then returns westwards to the Volga and extends along its right bank to the mouth of the Malyi Irgiz, rising somewhat to the east in the extreme lower reaches of this river. Thence, the border line again directed itself northwards, along the Volga floodplain, reaching the bend of the Samara; apparently, the southern border passes eastward along the Samara river (N.I. Larina) towards the Ural and joins the abovedescribed border, which passes from Siberia to the Ural [river]. Along the bottom land of the Ural and the rivers flowing into it (Burli and others), the marten goes down the river to Ural'sk and descends a little below it (transients known to Gur'ev; Sludskii, 565 1953). Extending eastward along the Ural river, the line joins the above-outlined southern border of the Siberian part of the range.

The western border of the European-Siberian part of the range throughout its whole extent from the Barents Sea to the Black Sea is formed by the state frontier.

The Caucasian portion of the marten's range occupies the forest regions of the Main Caucasus range northwards, including the foothill forests. The range apparently also includes the forests of the Terek valley lying on the plain. Information on the marten in the Parabochevsk forest near Shelkovsk station and in the mixed forest tracts of the Terek valley (Heptner and Formozov, 1941) relate, evidently, to this species. In the west, the range includes the basin of the Pshekha river (left branch of the Belaya), and perhaps

extend somewhat farther. To the east, the range reaches the interior forests of Dagestan in the basin of the Avarsk Koisu (Dinnik, 1911). Marten also occurs, apparently, in the foothill forests south of Makhachkala, but positive information on this is absent. Its absence is sometimes even emphasized there, for example, in the Deshlagara region (Dinnik, 1911). The range also includes all of the wooded southern slopes and the foothills of the Great Caucasus eastwards almost to Zakatal and Nukha.

In the Little Caucasus, the range occupies only the western part of the territory, namely the northern slopes of the Adzhar-Imeretinsk and Trialetsk ranges from Borzhomi and Bakurian' to the Belyi Klyuch. To the east of Akstafa-Chai and Debeda-Chai, *i.e.* the meridian centering on Lake Sevan, this marten is absent or extremely rare. They do not occur in the forests of Karabakh. To the south, along the Pri-Black sea region (Adzhariya) the range extends to the state frontier and along the Tavr, exits into Asia Minor. In all remaining part of the Caucasus, the pine marten is absent (Dinnik, 1910, 1915; Satunin, 1915; Vereshchagin, 1947, 1959). Old information on occurrences farther to the east, particularly at Talysh (Radde, 1886; Satunin, 1896) were denied by all subsequent authors. However, the latest data on occurrence of this species in Iran (see below) do not exclude the possibility of their appearance in Talysh.

Indications of occurrence in some parts of the Tien Shan (Shnitnikov, 1925, 1936; Shostak, 1927; N. Severtsov, 1873; Zarudnyi, 1915; Laptev, 1929) and even in Trans-Baikaliya (Cherkasov, 1867) are completely wanting in foundation.

The marten represents a stenotopic forest animal, connected to a significant degree, with forests of tall trees. In connection with this, its distribution maintains a more or less continuous character only in the northern parts of the forest zone. The farther to the south, the more it becomes sporadic, in accordance with the relative area and dispersion of forest massifs. In the forest-steppe and steppe zones, as has been indicated, its distribution assumes an extreme form of separate islands located far from each other. At the present time, in connection with rapid changes in natural conditions its distribution is becoming all the more sporadic in the north.

In most parts of the marten's range, if we do not take into consideration the several reductions associated with landscape

changes, as for example, the felling of forests, it was not, and is not now subjected to evident changes. The described range is the present species range, in all events in the European part of the Union and the Urals.

As for the Trans-Ural and western Siberia, the history of the marten's range is, apparently, more complicated. In the literature, there are quite a few assertions that earlier the marten was not distributed beyond the Urals and that the range of the species then increased eastward (Heptner, 1936, from data of L.G. Kaplanov; Skalon and Raevskii, 1940; Sludskii, 1953 and others). Concerning this, it is considered that this process was not far back in time—the last century and particularly at the beginning of the present one, and that earlier, the marten was not present beyond the Urals. The reason for this phenomenon is usually considered to be the sharp reduction in the number of sables and its extermination in several districts. With this, a suitable ecological niche for 566 the marten was freed-up. With a normal number of sable, the marten could not penetrate into the east because of its "resistance". It has been considered that the cause might be change in natural conditions—a shift in the black taiga through thinning, or both conditions together.

Analysis of literature records of the 18th cent., half-forgotten or considered unreliable, and of new archival materials (Kirikov, 1958, 1960), shows, however, that in West Siberia, the marten was already known a long time ago. Thus, in the 17th cent., it lived here along the border of the forest zone and throughout the foreststeppe in quite considerable numbers and still remained in the 18th cent., though in very small numbers. Pallas also took note of the marten near Tara. The marten existed not only in Tobolsk and Tara counties of that time, but even in Tomsk, i.e. farther east than now. Moreover, in the northern part of the West Siberian taiga (Berezovsk county), marten was absent in the 17th cent.; it was also absent in the middle section of the taiga zone—in Surgutsk county (1630, 1650, 1660) or it was met with here very rarely (Kirikov, 1960). Evidently, marten was distributed in southern Siberia far to the east, but in the north, it, apparently, did not reach the [Trans-Ural] plain.

Apparently during the 18th and 19th cent., marten (as well as sables) completely or almost completely disappeared in a significant part of its previous West Siberian range. It is difficult to understand the complete disappearance of information about this

species in the literature of the 19th cent., or, on the contrary, the reference to its appearance (settlement) in western parts of the country (Pelymka; Slovtsov, 1892 and others) at the end of the century.

On the basis of all these referenced materials, the history of the marten range in western Siberia more correctly presents the following aspect: in southern regions—along the southern part of the forest zone, the marten lived in the forest-steppe from time immemorial (fossils are known 2,500-8,000 years in age; Laptey, 1958) and reached Tomsk district. In the north of western Siberia, the marten was absent. Then, in connection with its destruction in subsequent centuries, the range of the marten contracted very strongly, it disappeared or almost disappeared in western Siberia. In recent times, the range is being re-established, especially intensively in the last decade. However, the full range in the south is still not re-established. In northern Siberia, the marten is settling in new regions, where, previously, it was absent. There, colonization has been taking place, in our day, especially intensively in the 30's. Therefore, externally similar phenomena have fundamental differences.

The reasons for these changes in range are not understood in detail and require careful investigation; evidently, both of the above-mentioned phenomena—biocoenotic (relationship between sable and marten) and changes of the landscape are significantly involved. In the south, where the marten lived earlier, the extermination of sable and decrease of its numbers were, probably, more significant; in the north, equally with the biocoenotic factor, change in the character of forests was, apparently, the main factor. The replacement of sable by marten under certain conditions in some regions is definitely known (Cherdynskii Ural and other places). Naturally, all these events went forward in a background of exploitation, its greater or lesser intensity, and changes in its form.

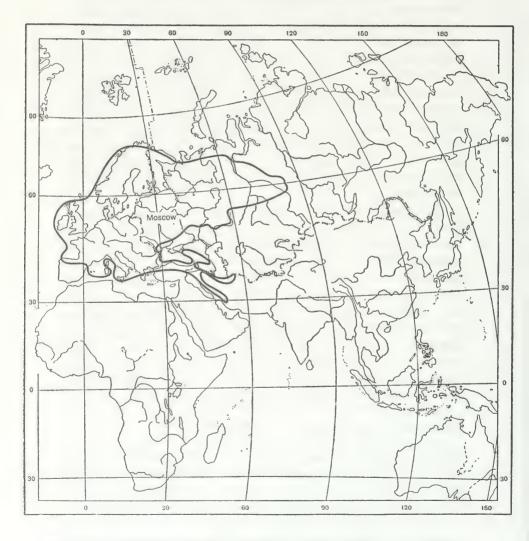
Geographic Range outside the Soviet Union

The range extends through Europe; in the west, it includes Ireland and England; in the north—the Scandinavian peninsula to tree line; and in the south—northern spain (Pyrenees), the Balearic Islands, Sardinia and Italy, Sicily and southwards in the Balkans at least to northern Greece.³⁴ In Asia, the range occupies Asia Minor

³⁴In Van den Brink (1958) the Balkans are excluded from the range. Marten, however, occupies all of Yugoslavia in the south including Macedonia (Dulich and Tortich, 1960). There are no data on its penetration farther to the south.

and northern Iraq, and to Iran in two extensions—along the Elburz system, it extends to the meridian of Budzhnurd [Bujnurd] in Khorassan and from Kurdistan and Luristan southeastward along the Zagros mountains approximately to the meridian of Shiraz (Misonne, 1959).

Information about its occurrence in northeastern China, where the pine marten is supposedly even more common than sable, and is sold as a low quality sable in the former Manchuria and China



567 Fig. 212. Species range of pine marten, Martes (Martes) martes L. V.G. Heptner.

567 (Sowerby, 1923) is deprived of any foundation. The reference applies, of course, to the true marten (see in particular Lukashkin and Zhernakov, 1934). References to the occurrence of marten "in Siberia, Turkestan to Manchuria" are also improbable (Brass, 1926) (V.H.).

Geographic Variation

Geographic variations of pine marten inhabiting our country have been discussed by several authors (Satunin, 1914; Ognev, 1931; Kuznetsov, 1941; Yurgenson, 1947). These studies dealt with both the entire range as well as its separate parts. The scheme, established about 20 years ago, has not been modified since then, and cannot be considered completely satisfactory. Some populations, characterized by highly subtle characters were given separate names. These features do not reflect equal representation of "good" subspecies, and several are *a priori* doubtful. The characteristics of marten skins as a commodity fur, apparently, served as the stimulus for distinguishing some forms.

A new revision of geographic variation in the species is necessary. The scheme of B.A. Kuznetsov (1941, 1952) is presented below with a few modifications, critical remarks and nomenclatorial changes. The diagnosis is given in brief format, sometimes with supplements from other authors.

1. Western European pine marten, M. (M.) m. martes Linnaeus, 1758 (syn. sylvatica, sylvestris, abietum).

Size large, tail long. Skull large and massive.

Fur on spine beautiful dark-chestnut color; guard hairs dark-brown, underfur bluish-gray, tips lighter and paler. On sides, fur slightly lighter. Withers and upper part of neck and head somewhat darker than spine. Muzzle brownish, slightly lighter posteriorly. Throat patch usually bright yellow. Belly dark brownish, darker than sides of body. Base of tail same color as back, to brownish toward its tip. Feet dark-brown. Pelage fluffy and fine.

Body length of adult males 480-530 and to 550 mm, of females 400-450 mm; tail length of males 250-280 mm, females 230-260 mm (Schmidt, 1943; Middle Europe).

Condylobasal length of male skull (22) 81.0-M $86.26 \pm 0.46\text{-}$ 88.0 mm, of females (9) is 77.0-M $79.00 \pm 0.70\text{-}83.0$ mm; zygomatic width of males 46.0-M $48.82 \pm 0.67\text{-}53.8$ mm, of females 42.3,

M 45.01 ± 0.70 –49.2 mm; skull height of males is 30.8–M 32.77 ± 0.25 –33.7 mm. Weight of 100 skins 10.5 kg (Kola Peninsula).

In western European part of the USSR eastward to Kiev, Bezhitsa, Smolensk, Vitebsk, Leningrad; Kola Peninsula and northern Kareliya.

Outside the USSR—western Europe, except the Mediterranean region.

The identity of Kola martens with our western and southwestern ones is highly doubtful.

Kola martens are the most valuable form of our martens.

2. Middle Russian pine marten, M. (M.) m. ruthena Ognev, 1926. Dimensions smaller than in preceding form. Skull smaller and less massive.

Prevailing color light reddish-tawny ("reddish sandy" in terminology of furriers). Back also such color, guard hair reddish-tawny, underfur light bluish-gray with reddish-tawny hair tips. Sides lighter and grayer than back, underfur on the sides also such color as back, but with pale hair tips. Belly darker than sides, tail at base colored like back; at end reddish-brown. Distal part of legs darktawny. Throat patch reddish. A small number of marten are found with chestnut guard hairs and light-blue underfur.

Body length of [adult] males 415-M 433-452 (and to 500 mm), length of tail 195-M 218-260 mm (Yurgenson, 1947).

Condylobasal length of male skull (32) 75.3–M 80.19 \pm 0.42–84.8 mm, of females (18) 71.1–M 74.71 \pm 0.55–77.3 mm; zygomatic width of males 41.4–M 44.36 \pm 0.36–49.0 mm, females 38.2–M 42.22 \pm 0.32–44.3 mm; skull height of males 27.4–M 31.07 \pm 0.14–33.3 mm, females 27.0–M 28.84 \pm 0.28–31.1 mm.

In middle districts of the European part of the USSR south to the range border (steppe) and on the north to the Vologda-Gor'kii-Kazan line.

Absent outside the USSR.

3. Northern pine marten, M. (M.) m. sabaneevi Jurgenson, 1947 (syn. borealis).

Dimensions, and characteristics of skull as in preceding form. Fur on back in most cases light grayish-tawny, guard hairs light-tawny without reddish tint, underfur light, ash-gray with pale hair tips. Tail tawny, lighter at basal part and darker at tip. Legs dark-tawny. Throat patch light-creamy or pale-yellow, rarely pure white. Pelage fluffy and soft.

569

Dimensions similar to preceding form. Body length of martens of upper Pechora (67) 380–M 433–460 mm; tail length 170–M 198–235 mm. Weight (42) in winter 580–M 784–1090 gm (Yurgenson, 1947). Weight of 100 skins 8.5 kg.

In European part of the USSR north of the Vologda-Gor'kii-Kazan line, except northern Karelia and Kola Peninsula, northern half of Urals (north of Sverdlovsk meridian), and West Siberia.

Absent outside the USSR.

Systematic relationships of this and the Middle Russian form are not completely clear (distribution after B.A. Kuznetsov).

4. South Ural pine marten, M. (M.) m. uralensis Kuznetsov, 1941.

Dimensions of body and skull large, near those of western European marten and larger than those of Middle-Russian.

Predominant color light grayish-tawny tone with highlights of reddish tones on rear part of back. Guard hairs on back light grayish-tawny, underfur light-gray with whitish or pale hair tips. Withers somewhat darker than back, sides lighter than back with whitish underfur showing through strongly. Throat patch very light, almost white to often white. Ends of feet brownish, tail base same color as back, its tip dark-tawny. Fur fluffy and soft.

Condylobasal length of male skull (7) 79.8–M 83.57 \pm 0.78–87.0 mm, female (2) is 74.9–75.0 mm; zygomatic width of male 45.0–M 47.14 \pm 0.43–49.1 mm, female 43.0–M 43.6–44.2 mm; skull height of male 31.8–M 33.0 \pm 0.41–34.9 mm, female 29.4–M 30.5–31.6 mm. Weight of 100 skins 9.5 kg.

In southern Trans-Volga, Bashkiria and Urals south of the Sverdlovsk meridian (B.A. Kuznetsov).

Absent outside the USSR.

Systematic relationships of the Ural marten with the Middle Russian and northern ones are, in some respects, not quite clear. The South Ural forms are characterized by reddish tone on the posterior part of the back which are not developed in the other two forms (B.A. Kuznetsov).

5. Caucasian pine marten, M. (M.) m. lorenzi Ognev, 1926. Dimensions very large, skull large and massive.

Color dark-tawny with reddish-olive tint. Guard hairs on back tawny, undercoat bluish-gray, moderately dark, hair tips sandy-yellow. Sides lighter than back with a grayish tint. Belly brownish-tawny with reddish strip along the mid-line. Feet dark-brown. Throat

light-orange or bright-orange, rarely yellow. Basal part of tail dark chestnut, tip brownish.

Body length 50-58 cm, tail length 23-25 cm, and [hind] foot length 8-9 cm.

Condylobasal length of male skull (38) is $43.1\text{-M}~82.36 \pm 0.62$ mm (85.3 mm)³⁵–53.0,* females (14) is $74.6\text{-M}~75.43 \pm 0.45$ mm (78.3 mm)–81.2; zygomatic width of males 43.1, M 47.42 ± 0.45 mm (50.9 mm)–53.0, females 41.2—M 44.14 ± 0.50 (43.7)–48.3 mm; skull height of males 28.4—M 31.87 ± 0.33 (32.1 mm) –34.0 mm, females 28.1–M 29.93 ± 0.31 (29.5)–31.8 mm. Weight of 100 skins 11 kg.

In Middle Caucasus and Trans-Caucasus.

Outside the USSR—in contiguous parts of Turkey and Iran. A well characterized race.

* * *

Outside the boundaries of our country, the following forms are usually recognized: 1) *M.* (*M.*) *m. latinorum* Barrett-Hamilton, 1904—Italy (except southern), Sardinia, Balearic Islands; 2) *M.* (*M.*) *m. notialis* Cavazza, 1912—South Italy south of Abruzzi (V.H.).

570 Biology

Population. The pine marten, restricted in its distribution to the forests of the European part of the USSR, is relatively few in numbers. The entire size of the population of this species before the October Revolution was approximately 40 thousand individuals or a little more. The number of pine marten greatly increased after the October Revolution. Very approximately, its numbers may now be considered equal to 200–300 thousand. Some estimations of numbers of the pine marten refer to tannery figures for the periods of irregular exploitation (1922–1925). The Northern Territory produced about 21% of the annual catch of marten skins; at that time, the western regions were considerably richer in martens than the eastern. The Urals produced about 16–17%; montane regions of the northern Caucasus—11%; Leningrad district—4%. These four harvest regions produced about 52% of the entire catch of the USSR.

 $^{35}\mbox{Average}$ dimension of adult marten (males and females) in West Caucasus (from Ryabov, 1958).

*Maximum and minimum values, male condylobasal length, clearly in error; too small. M may be correct—Sci. Ed.

The forest marten is, within its range boundaries irregularly distributed, a fact conditioned by the percentage of forested areas in the different regions and the degree of suitability of habitat (nutritional conditions, availability of prey items, nest and refuge conditions) within the forest tracts. Of no small importance are the relationships (relative weights) of lands of various values which are inhabited by the species with various densities.

Habitat. In all features of its structure and ecology, the pine marten is closely associated with forest. Within such forests, it reveals very significant plasticity in relation to external environmental conditions. It is encountered from the sparse pine forests of the Kola Peninsula and northern taiga to the oak forests of Mediterranean type, the "maquis" of Sardinia and tall beech forests of Adzhariya and Kolkhida.

Within the limits of such landscape zones are the most preferred habitats of the pine marten. In the coniferous forest zone, it is obviously attracted to dark coniferous forest. Most often these are old, large-trunked, multi-layered spruce stands in hilly regions. Less preferred, because food-poor and less suitable for nesting, are "even-age" spruce, with their single-age, most often slender, trunks. In the pine forests, the number of martens is not distinguished by stability because of instability of food reserves and the ease with which marten are destroyed by hunters. In 1952-1958 in Arkhangelsk district, in the spruce forests the tracks of pine marten were met with twice as often as in pine forests and other plantations. A series of daily trail surveys showed that 81.5% of the total length of trails are found in the spruce forests, 11.4% in pine forests and only 7.1%—in other plantations. These distributions changed in the different seasons depending on characteristics of distribution of the food resources.

In the zone of mixed forests, the pine marten prefers spruce-broad-leaved forests, oak groves, linden forests, and among the spruce forests—complex spruce forests, the spruce-aspen forests and the so-called pine-spruce aggregations (pines, spruce-mountain sorrel, and spruce-bilberry). In the zone of the broad-leaved forests, it prefers the large broad-leaved forests and their combination with montane pine forests, in the montane forests of the northern Caucasus, the fir-beech and beech forests, and the forests lying at their upper limits. Class I quality areas here are the fir forests of the lower, middle and sub-alpine belts (usually these are mixed

fir-beech or beech-fir forests). Class II quality areas are oaks, beech, pear, chestnut, aspen and alder groves in the broad-leaved [forest] zone (Ryabov, 1958).

Quality (bonitet) of habitat for pine marten regularly increases from north to south parallel to the change in forest biogeocoenoses and simultaneously with shifts in the nutritional regime. The ecological optimum of the species lies in the montane forests of the northwestern part of the Main Caucasus range. This demonstrated regularity is determined, first of all, by the feeding habitat.

Food. The pine marten belongs among the group of polyphagous carnivores, and therefore its existence does not depend upon the abundance of any one type of food. The following are among the most important foods of pine martens:³⁶ 1) mouse-like rodents (mainly red-backed voles); 2) squirrels; 3) birds; 4) insects; 5) forest fruits (including berries and nuts).



Fig. 213. Pine marten. Caucasian Preserve. Photograph by L.S. Ryabov.

³⁶Occurrence in food of 20% or more.

The relative weight and species composition of the food is highly variable. Each locality and each season is characterized by its own food set and by the relative weight of each. From year to year they also do not cease to vary. Nutrition variation depends on the geographic situation of the locality which all the more determines the specific composition of the food and on the time of year, which are connected with the presence of food and the degree of its availability for pine marten, and finally on the abundance (yield) of each food type.

There is a definite regularity in geographic variation of pine marten foods—carnivory of the diet increases from south to north, and omnivory—from north to south. This is also reflected in variation of the chewing apparatus (Yurgenson, 1951). From north to south, mammals and birds, especially tetraonids, as well as bird eggs regularly decrease in the food of the pine marten. On the contrary, occurrences of mouse-like rodents among mammals, and of insects increase from north to south.

In the coniferous taiga, plant food is of more frequent occurrence in the snowless period of the year. On the contrary, in the zones lying more to the south—in the snowy period. Its average yearly occurrence is similar everywhere and reflects the plant food requirement of the animal.

Seasonal variation of food is also well illustrated. For example the squirrel mainly occurs in pine marten food in the snowy period, constituting about 44% occurrence or more while in the snowless period—not more than 6–8%. The same may be said about tetraonid birds and mountain ash berries. On the contrary, insects, bilberry and mouse-like rodents are predominately typical food in the snowless period, while in the snowy period, they, except the latter, disappear, or are met with significantly more rarely.

There is a marked sexual dimorphism in foods of the pine marten. In the food of the weaker females, which are of smaller size and weight, hares, capercaillie, black grouse *i.e.* the larger prey are not met with. On the contrary, hazelgrouse and mouse-like rodents are more frequently encountered in the female's food than in the male's (Yurgenson, 1947; Gribova, 1958).

Data of geographic and seasonal variations in foods are presented in Tables 57 and 58. In these, 2,751 data points on nutrition of pine martens were used: 1) Lapland—587 (Nasimovich, 1948);

2) upper Pechora—593 (E.N. Teplova and P.B. Yurgenson)*; 3) Vologodsk district—205 (Gribova, 1958); 4) Zhiguli—151 (P.B. Yurgenson)*; 5) the middle zone—220 (Grigor'ev and Teplov, 1939; Yurgenson, 1939); 6) Northern Caucasus—1300 feces and 54 stomachs (Donaurov and Teplov, 1938; Ryabov, 1958).

From year to year, depending upon the abundance and degree of availability of one or another food, its occurrence in the food fundamentally changes. In the upper Pechora (Teplov, 1960) for 10 years (1937/38–1948/49), the occurrence of basic food types changed within the following limits (Table 58).

In Table 59 only the average occurrence of the different components of the food by seasons is given.

Table 57. Foods of pine marten of different geographical regions for the whole year (% of occurrence)

Food type	Lapland	Upper Pechora	Middle zone	Zhiguli	Northern Caucasus
Mammals	70.3	63.5	48.7	83.0	62.3
Mouse-like rodents	34.3	34.9	24.7	72.0	58.3
Squirrel	3.1	26.3	11.6	9.3	_
Insectivores	4.4	6.7	4.9	_	3.0
Birds	34.8	30.6	21.5	4.0	18.0
Including tetraonids	23.0	15.7	7.4		_
Bird eggs	6.9	5.7	4.1	_	0.6
Insects	10.5	10.7	7.4	24.0	39.5
Plant food	23.9	25.5	No data	14.6	14.8
Fruits (including berries)	17.5	11.6	No data	12.8	14.8

Table 58. Foods of pine martens in the upper Pechora over 10 years

Food type	% of oc	Average, %	
	Minimum	Maximum	
Voles	7.8	29.4	23.3
Squirrel	13.7	58.1	36.8
Tetraonid birds	4.0	24.0	15.1
Other birds	0.0	23.0	8.3
Plant food	5.0	39.1	24.5
Other food	6.1	20.9	11.8

^{*}No year given-Sci. Ed.

Table 59. Seasonal variation in foods of pine marten (% occurrence)

Zhiguli 84.4 77.7 7.7 7.7		Sno	Snowy period				ļ	Snow-f	Snow-free period	
80.9 84.6 80.5 38.1 82.2 93.1 58.9 84.4 37.7 52.6 50.0 36.2 53.3 87.5 44.5 77.7 7.0 16.4 14.7 6.6 2.8 1.0 7.7 13.2 1.1 5.8	 Upper	/olgodskaya district	Middle	Zhiguli		Northern Caucasus (stomachs)	Lapland	Upper Pechora	Zhiguli	
37.7 52.6 50.0 36.2 53.3 87.5 44.5 77.7 7.0 16.4 14.7 — 6.6 2.8 1.0 7.7 13.2 1.1 5.8 — — 2.8 1.0 4.3 26.3 5.5 — 0.7 4.5 4.8 4.6 — 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 14.1 22.1 — — 6.3 12.0 — 6.0 3.6 5.5 — — 6.3 12.0 — 6.0 3.6 5.5 — — 3.5 8.2 — 6.0 3.6 5.5 — — 3.5 8.2 — 1.3 7.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 — No data — — — — — — 9.0 No data — 10.1 — — — — - — — — — — —	70.8	80.9	84.6	80.5	38.1	82.2	93.1	58.9	84.4	70.1
7.0 16.4 14.7 — 6.6 2.8 1.0 7.7 — 13.2 — 0.4 — 7.1 — 13.3 — 0.4 — 7.2 — 13.3 — 0.4 — 7.2 — 13.3 — 0.4 — 7.2 — 0.7 4.5 4.8 4.6 — 7.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 5.5 — 0.7 4.5 19.4 33.5 2.5 2.5 27.3 5.5 — 0.7 4.5 19.4 33.5 2.5 2.5 27.3 27.3 5.5 — 0.7 2.1 — 0.3 12.0 — 2.8 15.3 29.0 30.1 11.3 — 11.3 — 12.5 — 0.7 — 6.0 — 0.7 — 6.0 — 0.7 — 6.0 — 0.7 — 0.7 — 0.0 data — 11.3 — 11.3 — 10.4 19.8 — 0.0 — 0.7 — 0.0 —	26.6	37.7	52.6	50.0	36.2	53.3	87.5	44.5	7.77	9.59
13.2 1.1 5.8 — 2.8 1.0 4.3 2.6.3 5.5 — 0.7 4.5 4.8 4.6 — 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 5.5 — 6.0 3.6 5.5 — 6.3 12.0 — 6.0 3.6 5.5 — 6.3 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 18.5 No data 7.7 41.5 — 6.0 — 6.	44.5	7.0	16.4	14.7		9.9	2.8	1.0	7.7	
13.2 1.1 5.8 — 2.8 1.0 4.3 26.3 5.5 — 0.7 4.5 4.8 4.6 — 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 14.1 22.1 — 6.3 12.0 — 6.3 12.0 6.0 3.6 5.5 — 8.8 15.3 29.0 30.1 13.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 9.0 No data 47.0 41.5 — 6.0 No data — 10.1 — 0.7 — 6.0	9.0		1	1		13.3	I	0.4	1	ł
13.2 1.1 5.8 — 2.8 1.0 4.3 26.3 5.5 — 0.7 4.5 4.8 4.6 — 2.8 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 2.5 2.5 2.5 2.5 2.5 2.5 2.5 2										,
26.3 5.5 — 0.7 4.5 4.8 4.6 — 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 2.5 27.3 20.0 3.6 5.5 — 6.3 12.0 — 6.3 12.0 — 7.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 19.0 No data 47.0 41.5 — 6.0	0.4	13.2	1.1	5.8		1	2.8	1.0	4.3	0.2
27.3 36.4 5.8 6.3 42.2 19.4 33.5 2.5 14.1 22.1 — — 6.3 12.0 — 6.0 3.6 5.5 — — 3.5 8.2 — 1.3 7.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 9.0 No data 47.0 41.5 — — 6.0 — No data — 11.3 — 0.7 — 6.0 — — — — — — —	8.8	26.3	5.5	ļ	0.7	4.5	4.8	4.6	Į.	3.7
14.1 22.1 — — — 6.3 12.0 — — 6.0 3.5 12.0 — 3.5 8.2 — 3.	28.2	27.3	36.4	5.8	6.3	42.2	19.4	33.5	2.5	22.3
6.0 3.6 5.5 — 3.5 8.2 — 3.1 8.8 15.3 29.0 30.1 1.3 7.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 9.0 No data 47.0 41.5 — 0.7 — 6.0 No data — 11.3 — 10.4 19.8 — 10.1	19.4	14.1	22.1		1	l	6.3	12.0	1	1
1.3 7.7 5.8 3.1 8.8 15.3 29.0 30.1 18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6 — — — — — — — — — — 12.5 — — — — — — — — — — — — — — — — — — —	9.1	0.9	3.6	5.5			3.5	8.2	l	
18.5 No data 50.0 65.6 40.0 19.4 21.0 14.6	1.6	1.3	7.7	5.8	3.1	8.8	15.3	29.0	30.1	14.8
9.0 No data 47.0 41.5 — 12.5 — 6.0 — No data — 11.3 — 10.4 19.8 — — — 10.1 — — — — — — — — — — — — — — — — — — —	28.9	18.5	No data	50.0	9.59	40.0	19.4	21.0	14.6	14.8
9.0 No data 47.0 41.5 — 0.7 — 6.0 No data — 11.3 — 10.4 19.8 — — — — — — — — — — — — — — — — — — —	23.6	1				1	l	12.5	1	1
No data11.310.4	47.0	0.6	No data	47.0	41.5	l	0.7	1	0.9	0.9
	0.7	L	No data		11.3	l	10.4	19.8	į	0.2
		I	-	l	10.1	}		l		0.3

In Arkhangel'sk oblast, from 1949–1961, *i.e.* during 13 years, the occurrence of different foods was as follows (Grakov, 1962) (Table 60).

In one of the provinces of Sweden (Hëglund, 1960)*, the character of winter food and its variation (%) within a three-year period were as follows (1956/57–1957/58–1958/59)

44.9	(25.0-61.5%)
39.7	(25.6-60.7%)
7.7	(6.5-9.0%)
21.8	
7.7	
12.8	
	39.7 7.7 21.8 7.7

The occurrence of squirrel in marten food increased with the decrease in mouse-like rodents and vice versa.

From the tables presented, it is evident that even within the boundaries of one zone (in the European northern taiga), considerable variation in the degree of occurrence of the main food groups is observed. In particular, the range of variation in the separate food groups is more sharply marked in Arkhangel'sk district than in Pechora, because there (in Arkhangel'sk district) the occurrence of squirrel and plant food is lower. The latter results from the absence of nut pine "nutlets" in winter food. On the Kola Peninsula the differences are even more marked.

Table 60. Nutrition of the pine marten of Arkhangel'sk oblast during a period of 13 years

Food type	Occurrence, %		Average (m)
	Minimum	Maximum	
Voles	12.5	75.5	45.1
Squirrel	0	17.5	7.1
White hare	0	9.2	5.0
Insectivores	0	6.1	2.0
Birds	0	32.5	21.5
Including tetraonids	2.8	22.8	13.6
Bird eggs	0	10.5	3.4
Frogs	0	9.2	3.5
Berries	0	43.1	11.2
Mountain ash	0	17.0	3.2

^{*}Not in Lit. Cite-Sci. Ed.

Mouse-like rodents occur as the main food of pine marten everywhere, mainly voles, and among the latter, the bank [Clethrionomy glareolus] and red-backed [C. rutilus] voles. Only in the northwestern Caucasus, are they replaced by local species—bush voles [Pitymys spp.] and others. In the food of pine marten, mouse-like rodents are found even when their number decreases in the forest. High numbers [of voles] in the forest causes the concentration of pine marten in biotopes that are less characteristic for them, such as in glades, burns, along forest borders, etc. This situation also causes intensification of the autumn migration of young martens. Mouse-like rodents, especially together with secondary and occasional foods, ensures minimum nutrition for martens in famine years. In the snowless period of the year, when the capture of mouse-like rodents is considerably easier for martens, their relative weight in the marten's food increases.

Species composition of mouse-like rodents utilized by martens is variable. It depends not only on their species composition and relative abundance in the local forest fauna, but also on their relative availability: the more active wood mouse [Apodemus] is also ways less common. The forests of the Black Sea coast of the Caucasus constitute an exception where, in some places, other mouse-like rodents are absent.

In the past, there was a widespread belief that the pine marten feeds mainly on squirrels. From the tables presented above show that this is not the case; the pine marten can exist very well, where squirrels are completely absent, as for example in the Caucasus, where the marten thrives. Even now, after the establishment of squirrels in the forests of the northwestern Caucasus, the pine marten makes little use of this resource (6.6%). Moreover, in the taiga forest during the snowless period when food is significantly more available for marten than in winter, the importance of squirrels in its food sharply decreases. The destruction of young squirrels in the nest by martens is still not based on facts.

In the last years, the role of the pine marten (and also of the sable in Siberia) in reducing squirrel numbers has been strongly elucidated (Yurgenson, 1954; Ivanter, 1961; Grakov, 1962; Yazan, 1962). The relationship between the number and density of both species per unit of forest area, as well as the degree of abundance and availability of the marten's main food are of fundamental importance. On average, the Pechora marten (which feeds more on

squirrels than anywhere else) eats 8–10 squirrels per winter. In years when squirrels are very few and martens are, on the other hand, abundant, these carnivores may destroy up to 30–35% of all squirrels; in other years, the importance of squirrels is considerably lower. It is believed that in the European North (Grakov, 1962) the pine marten lacks the power to affect the dynamics of squirrel numbers and cannot determine their number. Marked losses in local populations of squirrels are only caused by marten in those rare years when the low number of squirrels is accompanied by a low number of the tetraonid birds and mouse-like rodents, while martens are, at the same time, numerous.

An abundance of squirrels in nature does not cause an increase in their occurrence in marten food, especially if there are many voles. As was noted in Pechora, increased occurrence of squirrel in marten food occurs in connection with the increased occurrence in nature of weak and sick squirrels.

In the nutrition of the pine marten of the European taiga and some parts of the mixed forest zone, tetraonid birds acquire an essentail importance, especially capercaillie [Tetrao], black grouse [Lyrurus tetrix], hazel grouse [Tetrastes bonasia] and willow grouse [Lagopus lagopus]. Among these birds, the hazel grouse is the most frequent prey of marten. Tetraonid birds are hunted by marten mainly in their snow burrows and night resting places and, therefore in summer, their occurrence in marten food decreases significantly and becomes more or less accidental. By means of tracks in the snow, it is frequently possible to trace the unsuccessful hunts by pine martens of capercaillie or hazel hen. The quantity of tetraonid birds in marten food usually increases in the years with a reduction in numbers of voles and squirrels. In Pechora, capercaillie and black grouse are only found in the food of the larger and stronger males. In the food of females, only hazel grouse are observed (Yurgenson, 1947). This also occurs locally in the Vologodsk district (Gribora, 1958). White hare also occurs only in the food of males. In the Central Forest Preserve, there were individual male-hare hunters specializing in tracking and catching hares. Their daily trails were often particularly long.

The capture of small birds is a characteristic feature of pine marten although their relative weight in the ration is quite small. This is determined by the small size of the prey. Among the birds hunted are hole-nesters: woodpeckers, tits and nuthatches.

Shrews in marten food are either an accidental element or an indication of sharp deficiency in principal food. Sometimes, common moles [Talpa europa] appear in the food of martens in certain winters and in fairly great numbers. This is connected with the death of moles through strong freezing of the taiga soil in years with little snow (Teplova, 1947). The eggs of tetraonid birds, mainly those of capercaillie, in winter food of marten is also due to special conditions. This is connected with the death of the embryo in the shell early in spring, due to the excessive cold, a situation which occurs only when the female leaves the eggs for a long time in the years characterized by the repeated occurrence of freezing weather throughout June (Teplov, 1948, 1960; Semenov-Tyan-Shanskii, 1959).

Sometimes, remains of frogs and their eggs are found among the remains of marten food in winter. This is observed in those winters with food deficit, when the carnivores find, somewhere in a thawing rivulet, an overwintering accumulation of frogs. In Tatariya, on the Malyi Cheremshan, tracks of martens were frequently observed proceeding along the river ice, where American mink hunted frogs. Usually, the mink left the frogs on the snow and the martens took them off (V.A. Popov).

In the southern parts of the species range, marten in the snow-free period eat a great quantity of insects, including wasps, bees, bumblebees, beetles (especially ground beetles). In the taiga and in middle zone forests, wasps, bumblebees and honey bees are often encountered. In the Caucasus, beetles predominate. In the taiga, the significance of this food group is naturally less, as the food objects are fewer. On discovering a tree hollow occupied by wild bees, the pine marten willingly and protractedly feeds on the honey and the bee larvae.

Plant foods are met with in taiga forests, chiefly in the snow-free period. Then, first place is occupied by bilberries. Other fruits, including even choke cherry are of secondary importance. Only in the upper Pechora do nut pine "nutlets" acquire very great significance in autumn and winter, naturally in years with a yield. They are usually found in martens' stomachs together with forest voles. Marten feed on mountain ash berries in winter far beyond correspondence with their presence and availability. It utilizes ash fruits quite moderately, especially when other food is found in great quantities. There, when nut pine is absent in the taiga, ash

fruits and other plant food appear in marten food in winter when principal foods are few (Grakov, 1962). In the southern parts of the range, fruits, especially in autumn and winter, have greater importance for marten than in the taiga. In the northwestern Caucasus, together with a whole list of wild fruits (including mountain) ash, those of yew, which are poisonous to man, are of essential importance.

Polyphagy is a very characteristic feature of the pine marten. It enables it, in case of a deficit of one food, to turn to another. However, the comparison of combinations in one stomach of various numbers of foods with the degree of fullness of the stomach and the fatness of the animal, shows that differences in daily rations is a negative feature, indicating insufficiency in the main full-value foods. The analysis of multiyear data on food of pine marten also shows that along with the existing relationship between the degree of abundance of basic foods in nature and the frequency of their occurrence in food, another relationship is present—decrease in the occurrence of one food group causes an increase in demand for another food group or groups, independent of the natural abundance of these foods in nature. On the whole, as a result of polyphagy in pine martens, deep and prolonged depressions in their numbers are not observed, especially in those places where the conditions are more favorable for their existence. However, though rarely, there are seasons when a majority of the main foods in nature exhibit low numbers and martens starve.

From Table 68 on foods of the pine marten it is evident that in the snow-free period, occurrence of mouse-like rodents, mainly forest voles, bird eggs, insects and their larvae as well as fruits, obviously increases in connection with more varied and more available food assortment. At the same time, the occurrence of the more difficult to obtain foods falls off: squirrels and tetraonid birds. It has been already mentioned above that apart from this general situation, there are some local deviations. Thus, in Arkhangel'sk district (Grakov, 1964) in summer food voles were found to constitute 70% of the data, birds—23.2%, insects—24.2%, fruits (including berries)—21.2%, and among birds, the importance of tetraonids declines and the role of the small birds grows, lizards also appear, and the role of shrews—a food of last resort and squirrel decreases.

The stomach of marten holds a quantity of food equal to 1/10 of the live weight of the animal—this is the optimal daily norm in nature. It is not often achieved. The fullest stomach contained 60-90 gm of food, but more often about 50 gm. The pine marten cannot eat more than one squirrel per day and, quite often, leaves a part of the carcass. For estimating the general provisioning of marten with food in a given year and season, the investigator is led by data on the average fullness of the stomach with food (by weight) and the number of empty stomachs. In the middle and northern taiga zones, marten feed less well than in the mixed forest zone. The average fullness of the [northern] Pechora marten stomach for seven winter seasons was 28.7% of optimal fullness and in the middle zone—80-95%, which constituted 50-70 and up to 90 gm. In Tatariya (Grigor'ev and Teplov, 1939), fullness is about 44% (32 gm). This all accords with geographic variation in marten nutrition in different sections of their habitat and the duration of the daily route. In Pechora marten, the average percentage of stomach fullness in winter for a seven-year period ranged from 14.6 to 51.1%, and the average weight (excluding empty ones)—from 10.6 to 37.1 gm. In Vologodsk pine martens (Gribova, 1958), the average weight of stomach content fluctuated in four winter seasons from 25.5 to 35.5 gm (average-29.3 gm); maximum was 126 gm (a frog and its eggs). In the upper Pechora, better fullness usually occurs with a predominance of squirrel and wildfowl, but at this time, the greatest percentage of empty stomachs is also encountered.

Home range. From the time of dispersal of the young, the pine marten spends its whole life within the boundaries of a quite clearly limited section of the forest—its home range. The territories of males and females most often adjoin. The litter usually remain until autumn within the mother's territory. With plentiful food, litters sometimes do not disperse in winter.

The dimensions of the home range directly depend on the quality of area located within its limits, and on the ratio of various types of lands lying within its limits as well as on the food supply in the given year and season. Territory and home range dimensions are geographically variable; they regularly decrease from north to south. For martens of the Kola Peninsula, their size ranges from 15–20 and upto 50 km², and for northern Urals (Uk-yu valley), 6 km². In the spruce forest massifs of the southwestern part of Kalinin

district (Central Forest Preserve), it averages 6 km² (from 3.9 km² to 9.2 km²) (Konchits, 1937; Yurgenson, 1937, 1939). In Babkovsk forest tract (on the border of Penzensk and Tambovsk districts)—4.4 km² (Yurgenson, 1939), in Zhiguly (P.B. Yurgenson), 4.0 km², in the montane forests of the northwestern Caucasus, the average area of the daily home range (11 cases) is 46.7 ha (Donaurov, 1949; Ryabov, 1959), in fir forests—from 32 to 72 ha. In certain cases, martens lived in isolated forest islands with an area of from 90 to 300 ha.

The territory of the home range is assimilated by martens in succession, and the same range may itself comprise places periodically visited by the marten in different hours of its diel activity period, or else, as its hunting area. Individual parts of the entire home range are not used for hunting and only serve for movement.

Burrows and shelters. The most preferred shelter of the pine marten is a hollow tree. In the zone of broad-leaf forests, an insufficiency of these hollow trees does not usually occur. Here, the forest marten settles in tree holes of different sorts with a diameter of 30 cm and more. The opening of the inhabited hole mostly occurs high above the ground (from 2–2.5 m—4–5 m; in the northern Caucasus—at a height of 10–20 m and more), but in certain cases, the entrance to the hole is situated in the main trunk; the presence of light-penetrating cracks in the hollow is not an obstacle to use.

In the zone of mixed forests, hollows inhabited by martens most often occur in long-standing thick-stemmed aspens, more rarely in those fir trees devoid of tops (crowns), or in other types. In the taiga zone, inhabited holes are found in the nut pine, spruce, fir and aspen. There, where tree hollows are rare (mainly in coniferous forests), the pine marten willingly occupies squirrel nests (dreys), more often, as a form of temporary shelter; having caught and eaten a squirrel, the marten lies down in its nest to rest. In rare cases, the female and her litter occupy the drey (Ognev, 1931). In the middle [forest] zone, it was observed that dreys are more often inhabited by small females. This is not observed in the Pechora basin. Squirrel dreys are mainly used by martens in the first half of winter. Thus, in Pechora basin in autumn, and in periods of little snow in winter, the martens use holes and dreys of squirrels. Marten very rarely conceal themselves in logs lying on the ground. In the second half of winter with heavy snow and cold, (from

January) the marten leaves these shelters and moves to the logs hidden in thick snow where it is safer and warmer. In Arkhangelsk oblast (Garkov, 1964), also in the first half of winter, they more often (57–95% of cases) use squirrel dreys and tree holes and in the second—they use wind-falls and spaces between roots (71–81%). When approaching a shelter, the pine marten rarely seeks to confuse its track (20.5% of cases), but approaches the shelter through the trees for not more than 50 m.

In the Caucasus preserve (Ryabov, 1959), out of 16 temporary shelters, 11 were located in hollow fir trees, 2 were in wind-felled trees, and the rest were in hollows of beech, aspens and in wind-falls. Nests of litters in this region always occur in tree hollows. In holes with litters bedding, except the remains of rotten wood, does not occur. In the Tatar Republic, the marten sometimes occupies logs placed in the forest for bees especially in second-growth, where hollows are few (B.S. Popov). Very rarely, pine marten establish themselves in rock clefts (Zhiguli).

In the winter time, small stores of food are sometimes discovered in holes. In such a way, holes inhabited by bees may be considered unique "larders" of this animal; the marten feeds on their honey for a long time, making beaten tracks to such holes.

Daily activity and behavior. In contrast to sable, the pine marten is an animal with a distinctly demarcated twilight-nocturnal type of diel activity. During the day, it is active only very rarely and sporadically; somewhat more often in the period of sexual activity; the young pine marten, however, can sometimes be seen in the day-time.

Leading a semi-arboreal way of life, the pine marten climbs trees, but not always and not everywhere. Its occurrence and movement in the crowns of trees is closely connected with, and the main form of, feeding on squirrels. It captures other types of food mainly on the ground. In the forests of Arkhangel'sk district, when they feed mainly on voles, only 1% of its diel movements were among trees (of 132 km). In the second half of the winter, this occurs somewhat more often (Grakov, 1964). There, where food of the forest stratum is particularly scarce (montane forests of the northwestern Caucasus), the pine marten almost exclusively leads a terrestrial way of life, elevating itself into the trees only in search of a hiding place or shelter, or to eat mistletoe berries (Ryabov, 1959). In a night, it climbs trees not more than 2–4 times. The

same is observed in the sparse northern forests (Kola Peninsula), where its terrestrial way of life is determined by the considerable distance between the trunks of trees. The arboreal mode of life of this animal is often associated with coniferous forests. In regions where sable and marten coexist, the latter are found in trees more often. On the ground surface, and especially under snow, it orients itself and moves about less well than the sable.

The character of pine marten movement in winter is determined by the state of snow cover, especially that covering the tree branches (*kuxta*). The abundance of much clinging snow makes the movement in the crowns difficult except in cases when the *kuxta* is frozen to the branches, making climbing in the crown easier for the marten.

The length of diel movements (tracks) is determined by the abundance and availability of food, and in winter, also by the state



Fig. 214. Caucasus pine marten in natural setting. Caucasus preserve. Photograph by L.S. Ryabov.

of the snow cover. Activity of the marten is closely connected with its feeding. When satiated, the marten stops hunting and lies up at rest. In severe frosts or snowstorms, when the hunting yield does not compensate the organism's outlay, the pine marten does not go out from its shelter for several days, even if it becomes hungry. At low temperature, the marten moves little within a small area, and lies down during the day, with slightly filled stomach.

As with area of the home range, the length of diel movements (tracks) are closely connected with the quality of land, with its food supply, and regularly decreases from north to south. In the forests of the Kola Peninsula, it ranges from 10 to 25 km (16 km on average) (Nasimovich, 1948); in Priozersk region of Arkhangel'sk district (Grakov, 1960), based on data from 36 paths over five seasons, it equaled 8 km. With insufficient food, length of the diel route in the Severnii Territory reaches 22 km, in foodrich years, it usually reaches 5.3-6.0 km and does not exceed 7 km (Semenov-Tyan-Shanskii, 1961). In the upper Pechora, the route has a length of from 2 to 6 km (4.2 km on average), in the spruce forests of the southwestern part of Kalinin district-from 0.6 to 5.5 km (3.1 km on average; Yurgenson and Konchits, 1937), and finally in the Caucasus preserve—from 0.6 to 3.2 km (2 km on average; Donaurov, 1948). In the northwestern Caucasus (Ryabov, 1959), diel movement is usually in the form of a broken line and rarely closed; the average length of 11 complete paths here is 2 km; from 580 year to year it changes only slightly. Female marten (and sable) are always less active than males. The average length of route is 2.57 km for males and 1.48 km for females; it ranges from 0.60 to 3.24 km.

Seasonal migrations and transgressions. The pine marten is a sedentary animal to a great degree. Even deficiency of food does not always oblige it to leave the range it has inhabited for several successive years. At the same time, local migrations by this animal are observed. In certain cases, it was observed that the pine marten follows migrating squirrels and appears in those forests where the latter are concentrated. Attracted by the abundance of voles in forest glades, burned areas or in fields, marten appear in these habitats, which are not typical for them.

Dispersal and migration occur primarily in young marten from litters at the time when they begin to break up at the beginning of winter. Adult individuals rarely take part in this. The greater the density of the marten population, the farther the young are obliged

to move in search of suitable, unoccupied areas. In particular, young relocate to habitats temporarily rich in squirrels and voles, or they gather at carrion. Old marten sometimes migrate from one place to another, their worn teeth requiring them to search for more available food. With the dispersion of young, expansion of the range may proceed.

Reproduction. Up to now, the time when pine martens attain sexual maturity is not completely clear. According to data from animal farms, the animals mature not earlier than the third year of life or, as a rare exception—the second year.

Of 52 young female pine martens in the second year of life, pregnancy was observed in 35% (Ryabov, 1958). In a 15-month old male, on July 18, the testes were found to be greatly enlarged. About 45% of all females in a population bring forth litters. In the Caucasus, the percentage of barren females in the third year of life and older is 18.7%. For Arkhangel'sk district, barren females comprise 22% (Grakov, 1964).

Estrus and mating take place from the end of June to the beginning of August, frequently from the end of July-beginning of August. In individual cases, estrus is delayed until the end of August. It commences somewhat later than in sable.

Generally, pregnancy (Manteifel', 1934; Starkov, 1947) lasts 236-237 days; from other data (11 cases), 254-256 and 258-274 days (Starkov, 1947). In kidas*, it continues 280 days (Portnova, 1941). Pregnancy extends through a long period of inhibited development (latent period). Its duration is variable. As a rule placetation, being connected with the resumption of sexual activity, and which is suppressed by September, takes place in March. The so-called false rut is dated to that time, i.e. an increase in excitement of the sexually mature animals which at that time become more active than usual, and the males follow the tracks of the females. In certain cases, some deviations are noticed: thus, in Pechora preserve, embryos 9 and 31 mm in length were found in martens killed on 9 and 20 January. This situation, and the presence of sexually immature individuals, explain why the false rut does not occur in all martens. A marten impregnated on 15 July in the German Federal Republic gave birth on 5 January after being transported to Argentina; the duration of pregnancy due to the latent period was shortened to 176 days (Ulrich, 1953).

^{*}See pg. 833.

From placentation to parturition, embryonic development in all our species of the marten family takes 27–28 days (Kler, 1941)³⁷. On farms, birth of young occurs in April (Starkov, 1947), or 22–26 March (Manteifel', 1934). In case of early placentation, parturition should take place in February.

581

The number of young in a litter ranges from 2 to 8, most often 3–5. Average size (for entire range) is 3.8; in the Pechora basin, it equals 3 (2–4), in Moscow district, 5 (3–7). In the northwestern Caucasus, litter size ranges between 2–7, usually 3–4 (Ryabov, 1958). The average size of the brood varies negligibly in different years: for Arkhangel'sk district and Komi ASSR, from 2.54 to 3.0 (according to corpora lutea of ovaries, 3.5–4.0); for Kirov district, it averaged 3.7 for 1959–1960 (Grakov, 1962).

Growth, development, and molt. Growth and development of the pine marten take place as in the sable. Weight increment in young marten decreases sharply with opening of eyes (30th to 32nd day), when the animals begin to feed independently. Further weight increases proceed regularly, but from 48 days of age, females begin to fall behind males in weight: at the age of 10 weeks, animals weigh 400 gm, at 20 weeks, male—700 gm, and female—600 gm; at 30 weeks, male—800 gm, and female—700 gm. At the age of 40 weeks (10 months), male—1050 gm, and female—850 gm. At the age of 15 months, the male attains adult weight. In winter, adult males weigh 1200–1400 gm and in summer, 1400–1650 gm. Females weigh 800–1100 gm and 1000–1350 gm, respectively. Replacement of carnassial teeth takes place from 21 July–8 August. Juvenile fur of the female is replaced by 15 September, and that of the male—by the end of that month.

Senses of smell, hearing and sight begin to appear in the 7th week of life. At that time also, coordinated movements and the typical gait, jumping, are initiated. Climbing ability develops in the 10th–12th week, when springing capability of jumping develops. Young marten begins to kill subadult rats independently in the sixth month of life, having begun to utilize meat as food at the age of six weeks (Schmidt, 1943;* Herter and Ohm-Ketner, 1954)*.

The pine marten molts two times annually—in spring and in autumn.

³⁷In badger and otter—about 60 days.

^{*}Not in Lit. Cit.-Sci. Ed.

Enemies, diseases, parasites, mortality, and competition. Dangerous enemies which in some way might significantly affect its numbers, are not known for pine marten. Among the predators which are sometimes successful in attacks on martens, especially young marten, are wolverine, red fox, golden eagle, white-tailed eagle, goshawk and eagle owl. In Kalinin district, remains of young marten were found in the nest of a buzzard [Buteo buteo].

Neither epizootics nor helminth infections obviously influence the number of pine martens. Only a small number of cases are known of infection with pulmonary helminths (filiaroidosis and kernozomatosis), which caused significant plague among pine martens in the Northern Caucasus and in Georgia, accompanied by a great reduction in their number. Pulmonary filiaroidosis infection and the epizootic caused by it were noted in Severnii Territory in 1951/52-1955/56 when the number of martens was high. Of 503 pine martens from Arkhangel'sk district (Grakov, 1964) investigated from 1946-1958, filiaroidosis was found in 55.3% and Skryabingulosis in 48.2%. Maximum intensity of the first infection was noted in 1951-1953, of the second, in 1953-1954. Seriously infected females die from filiaroidosis more often than males. Martens infected with filiaroidosis are also found to be intensively infected with Skryabingulosis. Adult females are infected with Skryabingulosis more heavily than adult males and the yearling of both sexes. Poorly nourished martens are always more strongly infected.

In large series of skeletons and skulls, a series of cases of healed broken bones of the limbs and caudal vertebrae were found; in one case—even a self-healed bullet wound of the cranium.

All predatory animals and birds inhabiting the forest may be considered as competitors of pine martens—red fox, forest wildcat [Felis silvestris], sable, stone marten and others. All birds and animals utilizing mountain ash, bilberry, stone pine "nutlets" and other plant food of marten may also be regarded, to some degree, as its competitors. Cases of interspecific competition for food which might have displaced the pine marten from its occupied habitat, or which influenced its number, are unknown.

In individual cases, the longevity of marten has reached 14–16 years. Under natural conditions, pine martens rarely attain such an age and their average longevity is much shorter.

The age ratio in separate populations is determined, first of all, by the intensity of exploitation. In a series of marten from Pechora-Ilvch preserve (76 specimens, Zoological Museum, Moscow University), marten up to one year old constituted 47%, up to two years old-41%, older than two years-9.2% and those older than three years—2.7%. In the same preserve, from material of commercial hunting for 1937/38-1948/49 (309 specimens), yearlings constituted 49.9% on the average (from 44% to 58%). In the following winter, after a winter with abundant food, an increase in the percentage of yearlings was noticed in the population. However, the rise in the percentage of yearlings may indicate not only the increase in the size of the annual increase but also an increase in mortality in older ages. Moreover, in the time of the harvest, a larger percentage of yearlings is usually captured than their actual proportion in the population. Of 464 martens commercially taken in the upper Pechora (Yazan, 1962), adult individuals of both sexes constituted, for a series of years, 35.4%, in particular, 24.5% males and 10.9% females; juveniles were 64.4%. Among the adult martens, the sex ratio was 1.0:0.4 and among those up to one year it was 1.0: 1.7. On the whole, males in Pechora population constituted 54% and females, 46% (Teplov, 1960).

Thus, considering the prevalence of young matens in the catch, as a normal phenomenon, and also that the preeminence in the harvest of males, the sharp decrease in the percentage of females in the population with the transition from yearlings to adults (1 year and older) draws attention to itself.

Of 126 martens taken in 1939/40 in Volzhsko-Kamsk Territory (Aspisov, 1959), juveniles constituted 51.6%, in their 2nd year [yearlings]—30.2%, in their 3rd year—11.9%, in their 4th year—3.9%, and in their 5th year—2.4%. Individuals above five years old were absent. In 1940/41, among 289 harvested marten, were juveniles—70.6%, yearlings—19.4%, in their third year—6.2%, in their fourth year—2.4%, and in their fifth year—1.4%. It is quite obvious that the percentage of juveniles in 1940/41 increased not only on account of the higher fertility, but also on account of the decrease in number of older individuals. The average percentage of juveniles, over several seasons, (594 individuals) was 54.4%, (42.9–70.6%). Males in this series constituted 61%. Males in this commercial catch always and everywhere predominated.

In Arkhangel'sk district (Grakov, 1964), after winters with conditions favorable to martens, the percentage of individuals up to one year [juveniles] in the catch increased to 59%, and after unfavorable winters, fell to 43–44%. With favorable conditions, the sex ratio in the population changed in favor of females (from 38% to 56%). In the unfavorable years, the percentage of pregnant females fell as much as 83% (Kirov district, 1959/60). This was also observed in Vologodsk district (Gribova, 1956). With three being the average number of embryos in Pechora pine martens at the beginning of the harvest, for each female there were two juveniles; mortality was 30%*. In the population, the average percentage of juveniles is 48% with annual fluctuations from 35% to 58% (Teplov, 1954).

In Arkhangel'sk district, during 13 harvest seasons (1949–1961), males exceeded females by 5.8–31%, averaging 7.2%. In 5 years of track counts (49 cases), males were 54%, and females — 45%. By means of a thorough, even complete exploitation of one area in the course of three seasons (102 data points), males were 54% and females 46% in the catch (Grakov, 1964). It was established (Grakov, 1964) that data from the harvested population sample, because of selectivity during harvest, the percentage of juveniles in the population was overestimated by 14%. Baited traps more often capture males, but hunting with guns assisted by *laika* dogs, which occurs at the start of winter, takes more females.

In the northwestern Caucasus (281 martens), juveniles constituted 55.2% (ranging from 49.9-58.2%), yearlings—31.7% (29.1–38.6%) and 2 year olds and older—13.1% (12.1–13.4%) (Ryabov, 1958). Males were 56.9% (54–58%), females—43.1% (42–45%). The number of males in the first year of life exceeds that of females 2–2.5 times.

In this way, the pine marten population is quite quickly restored. *Population dynamics*. The number of pine marten is subjected to oscillations which, however, are relatively small. High levels of populations are observed during considerable time intervals, about 9–11 years. Population stability is explained by the polyphagy of the pine marten.

Noticeable increase or decrease in numbers (in the absence of harvesting) is usually determined by the simultaneous abundance and availability of some of their principal foods, which does not

^{*}Rounded value-Sci. Ed.

occur often. This is predetermined by food abundance during several successive seasons combined. The rarity of such combined events determine the rarity of noticeable population changes. Usually, deficiency of one main food is compensated for by the abundance of another, or several other secondary foods.

Pulmonary infection has a place in depression of numbers, but is rare and does not constitute a universal phenomenon.

The most extensive filiaroidosis among pine martens of northern Europe was observed in years of favorable feeding conditions. but after unfavorable years. Skryabingulosis, less pathogenic for pine martens, differed in its greater intensity and extent during years with unfavorable feeding conditions. During the period from 1951/52-1955/56, the extent of filiaroidosis was determined to be between 83.7 and 100%, and Skryabingulosis in the period from 1951/52-1953/54 as 71-87%. A peak population of Arkhangel'sk pine martens was recorded in the winter of 1951/52, but the greatest number of dead animals was found in 1950/51 and 1954/55. The next rise in numbers was in 1957/58 (Gribov, 1959; Grakov, 1962). Helminthic infections are always due to decrease in the organisms resistance as a result of poor nutrition. It is not the ultimate cause of population changes, but one of the links in the process of decline. Harvesting is a very obvious, and sometimes the prevailing, influence on populations. With intensive harvesting, high numbers never occur. Under conditions of absence of hunting (preserves), the numbers of pine marten fluctuate within comparatively narrow limits—by a factor of 1.6 (Pechora: Teploy. 1951), and a factor of 3.2 (southwestern Kalinin district; P.B. Yurgenson) during 15-20 years.

In Pechoro-Ilych preserve (Teplov, 1960), during the period from 1938/39–1948/49, *i.e.* for 10 years, the frequency of occurrence of their tracks in pine forests along a 10-km route in winter fluctuated between an average of 0.5 to 0.95; *i.e.*, by 1.9* fold and in the region of dark coniferous forests, more favorable for the pine marten—from 0.8 to 1.3; *i.e.*, only 1.6 fold. In Arkhangel'sk district (Grakov, 1962) during eight years (1952–1959) this frequency fluctuated from 0.7 to 2.9; *i.e.*, 4.1 fold.

It is obvious that stability of population numbers serves also as an indicator of more stable and more optimal habitat conditions—especially in conjunction with a high level of numerical fluctua-

^{*} Misprinted as 19 in Russian original-Sci. Ed.

tions. In Arkhangel'sk district, the pine marten population is estimated to be plentiful.

If there are territories where the capture of pine marten is prohibited (preserves, many years of legal protection), the stable abundance of these carnivores is secured by a mixture of hunting areas, on account of pre-winter settlement by young marten from dispersing litters.

Field characteristics. It is rare to encounter a pine marten. 584 One may often observe the characteristic feces of pine marten on logs, stumps or on forest paths—sausage-like in form, length 8-10 cm with diameter about 1-1.5 cm. Usually, it is spirally twisted. Other than its dimensions, it is well distinguished by remains of small animals and birds (hair, bones, feathers), together with fruits and insects, and by the very palpable odor of musk. Sometimes, one may see the double footprints of the marten track on moist ground or on mud. These tracks are larger and more elongate than those of the forest polecat.

On snow, the tracks of pine marten are not clearly printed due to the dense fur on the food pads; in the stone marten, the callosities of the feet are always obvious in the footprints, even in winter.

The most typical gait of the pine marten is a bound, leaving on the snow an extended chain of paired footprints. Sometimes, the pine marten "trots" and in this case, its tracks are similar to those of hares. The pine martens rarely walks, putting one foot behind the other.

The length of the bound of a marten is 65-70 cm, and on ascending a slope, not more than 45-50 cm; when ambushing its prey, up to 35-40 cm. The size of the individual prints, and the length of leaps in females, are less than in males. The animal's sex is easily determined by the relation of urine spots to the path of the tracks (during one hunting course, the marten urinates 7-8 times; Nasimovich, 1948).

The marten sinks no deeper than 3-6 cm into snow. On jumping down from a tree, the marten's tail does not leave a mark as the sable's does (P. Yu.).

Practical Significance

In value to the fur trade, the skin of the pine marten is exceeded only by that of sea otter, beaver, and sable. Its fur is durable, warm, and beautiful. Due to its relatively small population and the



584 Fig. 215. Tracks of pine marten in short (130-150 cm*) leaps; the footprints are arranged in pairs and in fours. Talitsy, Moscow district. 18 June 1951. Sketch by A.N. Formozov, about 1/5 natural size.

difficulty of capture, the pine marten does not belong to the objects of mass exploitation. The greatest proportion of martens is hunted in the montane forests of the northern Caucasus. Here, the most valuable and larger martens are obtained. The trade of pine marten in the USSR constitutes about 25% of the world catch of martens (including stone marten).

Exhaustion of their stock as a result of overhunting has led to the necessary prohibition of its hunting everywhere. This measure was shown to be very effective and the prohibition was replaced

^{*} Inconsistent with figures given in text-Sci. Ed.

by licenced hunting, a measure which proved to be the best form of exploitation. In recent years, the stock of pine marten has not been fully exploited due to insufficiently experienced hunters and good hunting dogs.

The main methods for commercial taking of marten are: 1) shooting with the aid of hounds; 2) driving with the aid of hounds; 3) log deadfall traps (of the *kulemok* type—"torlo" "snettsi", etc.*; 4) metal jaw traps. The active method of harvest with the aid of a dog, is the most effective one, but for this, good dogs are essential. The period of harvest must be restricted to two months: December–January. The effectiveness of the various methods of capture for pine marten is only known for the northwestern Caucacus (Ryabov, 1958). Tracking after the first snowfall is most effective, especially in deciduous forests. Hunting with the aid of a *laika* dog comes in second place; harvest by snaring is third; fourth—using log deadfall traps and fifth—metal jaw traps. The average daily income of a hunter ranges from 8 roubles 12 kopecks to 3 roubles 18 kopecks depending upon the method of hunting.

Since the pine marten can adapt itself to cultivated landscapes and lives in small forest islands of few a hundred hectares, it can be a prospective animal in the hunting trade. With shelterbelts attaining mature growth marten would be able to establish themselves widely.

With the regulation of harvest, the number of pine marten is easily maintained at a high and stable level. Between 1926–1928 (Danilov, 1963), the catch of marten constituted about 1.8% of all furs obtained in the USSR. From 1956–1959, it comprised 3.4%. The demand for skins of pine marten in the world market is not stable and is determined by styles in fur (P.Yu.).

STONE MARTEN³⁸

Martes (Martes) foina Erxleben,** 1777

1977. Mustela foina. Erxleben, Syst. Regni Anim., 1, p. 458. Germany.

*Special sorts of traps—Sci. Ed.

**Misprinted in small lower-case type in Russian original—Sci. Ed.

³⁸Also, belodushka (white-breast), "kunitsa-belodushka" (white-breasted marten) and among furriers, kunitsa gorskaya (mountain marten).

- 1792. Mustela domestica. Pinel. Actes Soc. H.N. Paris, 1, p. 55. France.
- 1801. Mustela foina alba. Bechstein. Gemeinn. Naturg. Deutschlands, 1, p. 759. Thuringia, Germany.
- 1869. Mustela martes var. fagorum. Fatio. Faune vertebr. Suisse, 1, p. 318. Switzerland.
- 1873. Mustela intermedia. Severtzov. Vertik. gorizont. raspredel. Turkestansk. zhivotnykh. Izv. Obshch. lyubit. est., antrop. etnogr., 8, No. 2, p. 61. Karagodzhur in the sources of the Chu river south* of Issyk-Kul'.
- 1879. Mustela leucolachnea. Blanford. Second Yarkand Mission, Mammalia, p. 26. Yarkand, northwestern China.
- 1906. Mustela foina nehringi. Satunin. Izv. Kavk. muzeya, 2, p. 120, tab. 2. Tbilisi. Transcaucasus.
- 1911. Martes foina bosniaca. Brass. Aus dem Reiche der Pelze, p. 468. Bosnia, Yugoslavia.
- 1914. Martes foina altaica. Satunin. Opredel. Mlekopit. Ross. Imp. key for mammals of the Russian Empire. 1, p. 111. Altai.
- 1917. *Martes rosanovi*. V. et E. Martino. Zap. Krymsk. obshch. estestvoisp. lyubit. prirody, 7, 1 (reprint). Northwestern slope of Chatyr-Dag, Crimea (Crimean preserve; V.H.).
- 1946. Martes foina ognevi. Laptev. Izv. Turkm. fil. AN SSSR, 2, p. 57. Central Kopet-Dag, Bol'shoi Balkhan (type and type locality not indicated). It is assumed that the type locality is the central Kopet-Dag; (V.H.).

Diagnosis

Length of tail with terminal hairs somewhat more than half of body length. Color monotone, on throat and chest a sharply outlined patch of pure white color, varies in form and size, but which usually forms two projections directed backwards—to base of forelegs. Head not lighter than back. Bony tympanic bullae relatively short and widely separated. Longitudinal diameter of the inner half of the upper molar is only a little larger than the outer half (V.H.).

586

^{*}The river is west of Issyk-Kul'-Sci. Ed.



586 Fig. 216. Stone marten, or white-breast, *Martes (Martes) foina* Erxl. Sketch by A.N. Kamarov.

Description

The stone marten is similar, in its general appearance and many individual features, to the pine marten. It has, however, on average a somewhat longer tail, the head is more elongated, as if somewhat compressed laterally, anteriorly more pointed and, on the whole, not so rounded as that of the pine marten. Moreover, the ears of the stone marten are shorter and with more rounded tips. They are also widely separated (in the pine marten, the distance between their inner edges is about 47 mm, in the stone marten—54–56 mm; Schmidt, 1943). In stone marten, the bare tip of the nose is light, usually of light flesh-color or grayish; in the pine marten, it is dark-black or grayish-black (Schmidt, 1943). All these characteristics make the head form and "face" of each marten species quite different.

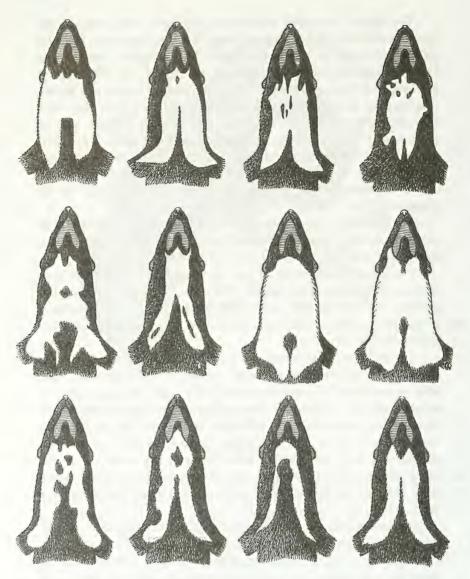
The feet of the stone marten are less furry than those of the pine marten, and do not look as broad. Even in winter fur the heel pads are obvious, as well as the digital. In summer fur, the legs are less fur covered, and the tail appears still longer; the difference in ear length is more noticeable. The stone marten stands and moves in a manner which differs considerably from that of the pine marten—they often appear to be "creeping" like the polecat, and do not bound ("gallop") as do the pine marten and sable. This, evidently, depends also on the fact that the length of the forelegs (height at the "withers") differs in each species—in the pine marten, it is about 15 cm, and in the stone marten—about 12 cm (Schmidt, 1943).

The pelage is coarser than that of the pine marten, with elastic guard hairs and less dense underfur. The summer fur is short, sparse and coarse, and the tail is lightly furred.

The general color tone of the fur approaches that of the pine marten, but is somewhat lighter. The underfur is also lighter—not grayish, but whitish. The tail is dark-brown; the color of the back 587 is darker than that of the pine marten. In the remainder, its color is like that of latter.

The differences in color and form of the throat patch of both species are very sharp. In the stone marten, it is always white, and only in the form of a rare exception has it light pale highlights. It is large and, as a rule, two projections extend backwards to the base of the forelegs and also extends upward on the legs, sometimes halfway. Thus, the dark color of the belly juts out between the forelegs as a line into the white color of the chest and sometimes into the neck. In the pine martens, on the contrary, the white color between the forelegs juts backwards as a protrusion into the belly color.

Numerous and various deviations from the described typical form of the patch occur, making it highly variable. Thus, the patch may have the shape of a bracket lacking the large anterior field, or sometimes dark spots are found in it, breaking down its form and greatly reducing its area. The patch is sometimes almost unnoticeable or absent (mainly in martens of Crete and Middle Asia). Finally, very large patches occur, of a more or less rounded form and not divided from behind. As indicated above, the form and color of the patch are also variable in the pine marten. Variation in this character in both species gives, in some cases, similar forms



587 Fig. 217. Variations in form of throat patch of stone marten, M. (M.) foina Erxl. Upper row—European marten, M. (M.) f. foina Erxl. (Middle Europe); middle row—first and third from left—Caucasian stone marten, M. (M.) f. nehringi Sat. (Vladikavkaz and Talysh), second and fourth from the left—Crimean stone marten, M. (M.) f. rosanovi V. et E. Mart. (Crimean preserve); lower row—Middle Asia stone marten, M. (M.) f. intermedia Sev. (Kopet-Dag). Drawings by N.N. Kondakov, after material of Zoological Museum, Moscow University (upper row, after Wehrli, 1932*, with modifications).

^{*}Not in Lit. Cit.-Sci. Ed.

of the patch. The use of this feature alone may lead to mistakes in identification and to mistaken concepts of distribution, especially of the stone marten (see below, "Geographic Distribution") and to an ungrounded confirmation concerning hybridization between the species.

On the whole, individual and geographic variations in color (not considering the patch) and fur quality of stone marten are less than in pine marten. In particular, there are not great changes in general color tone, and no tendency towards geographic localization is observed.

There is no sexual differences in color and character of the fur. Young animals in their first autumn have fur not differing from the coat of adults.

The skull of the white-breast is similar to that of the pine marten and differs from it chiefly in the following features: 1. Facial portion shortened (distance from posterior edge of suborbital opening to posterior edge of canine alveolus equal to or a little more than half of distance between ends of supraorbital processes). 2. In upper profile, facial portion of skull pulled down; therefore, convexity formed in interorbital region (frontal process—a feature better developed in adults and older individuals). 3. Nasal bones have a well-marked constriction ("isthmus") in their middle part (a character which is noticeable mainly in younger animals). 4. Constriction ("isthmus") on skull behind supraorbital process more sharply defined (lines, limiting skull in this region form an angle). 5. Bony tympanic bullae somewhat shorter and somewhat more widely separated, especially at their posterior part (length of bulla less, rarely equal to, distance between them at their middle part). 6. Projection at anterior edge of sphenopalatine notch absent or weakly defined. 7. Upper carnassial tooth somewhat larger (its length usually more than diameter of upper molar lying next to it). 8. General dimensions of upper molar relatively smaller and its inner blade considerably smaller than in pine marten. In linear measurements, this blade is only a bit larger than the outer one, rarely equal or almost equal to it. Its longitudinal diameter is considerably less than diameter of entire tooth. 9. On outer (lateral or posterolateral) surface of upper molar, there is a clearly defined vertical fissure (this tooth surface is evenly convex in pine marten). Characteristics of structure of upper molar are noteworthy for differentiation of skulls of the two marten species (Fig. 190).

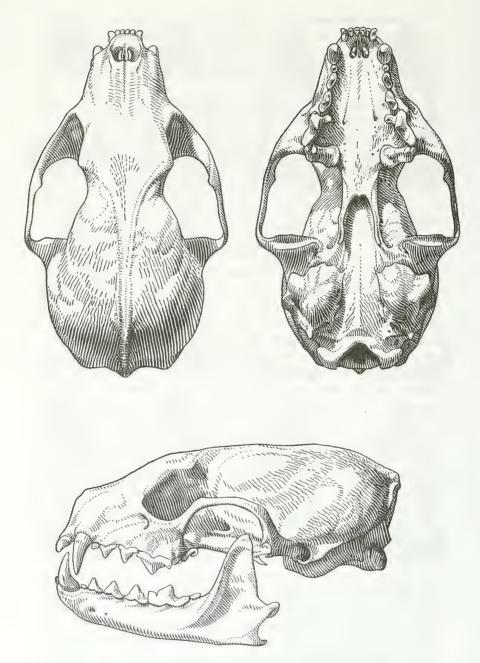


Fig. 218. Skull of stone marten, Martes (Martes) foina Erxl.

Sexual and age differences in the skull are the same as those given above for the pine marten.

The number of caudal vertebrae is 20–22 (Caucasus), *i.e.* as in pine marten (Yurgenson, 1956), although only 17–19 are usually recorded (Schmidt, 1943). Thorasic vertebrae are 14, lumbar, 6, pelvic, 3. Clavicles are smaller than in pine marten; their length is about 10 mm. As in pine marten, they are flattened, but they are all elongated, of identical width throughout their whole length and evenly curved (Shtreili, 1932).*

Differences in the structure of the male genital organs of both species are quite significant. The penis of the stone marten is 1900 larger—its preputial part is about 33 mm (Shtreili, 1932). The form of the os penis is the same, but larger and massive in its dimensions (see below); the os penis of a young stone marten is somewhat longer than that of an old pine marten. Moreover, the generally weak sigmoid flexure of the bone is somewhat more sharply displayed. In young martens, the bone is not only shorter, but also not thickened in its basal part, which character is well-marked in the adults.

The diploid number of chromosomes (2N) is 38 (Vorontsov, 1958).

The average dimensions of the stone marten are a little less

than the pine marten; however, this difference is very insignificant. Within the species (including Central European martens), dimensions are as follows (Ognev, 1931; Kuznetsov, 1941, Schmidt, 1943; Ryabov, 1958). Body length of males 430–590, of females 380–470 mm; tail length of males 250–320, of females 230–275 mm; length of hind foot of males 85–95 mm; height of ears of males 43–47 mm; height at shoulder about 120 mm.

Condylobasal length of skull of males 71.0–86.0; of females 73.2–82.8 mm; zygomatic width of males 42.2–56.4, of females, 43.6 to 50.6 mm; height of skull of males 30.1–32.6, of females, 29.1 to 31.0 mm (measurements of skull after data of Kuznetsov, 1941, 31 males, 29 females).

Weight of males in winter is 1700–1800, in summer the average is 2000–2100 and not more than 2400 gm, that of females in winter is 1100–1300, in summer 1400–1500 gm (German martens on farm; Schmidt, 1943). For Caucasian martens, it was shown (Ryabov, 1958) that weight of males in winter was 1070–M 1325–1950 gm, of females 865–M 1060 gm–1306 gm (20 specimens in

^{*}Not in Lit. Cit.-Sci. Ed.

all). These data, however, are very approximate, because they were obtained from skinned carcasses, "in a non-fresh form or after a long time in formalin." Weight of the fresh hide of a male (1) is 285 gm.

Length of the os penis of young martens (15 juveniles) is 50.6–M 54.8–58.2 mm; weight is 220–320 mg. In animals two years old and more (14), length of the bone is 56.0–M 60.0–66.2 mm, weight is 380–800 mg (Caucasian martens; Ryabov, 1958).

Dimensions of females are somewhat smaller than those of males. In body length, this difference is not, however, more than 100 mm (in the Central European martens). Dimensions are subject to negligible geographic variations. On the whole, variation in meristic characters within the USSR, as in color, is less than that in the pine marten (V.H.).

Systematic Position

The stone marten is a well-defined species. Regardless of significant similarity of features, it is relatively distant from the pine marten. In any case, these two species are more different from each other, than are the sable and pine marten. All "small" marten; i.e. all species of the genus Martes, except the kharza [yellow-throat marten] (M. flavigula) and il'ka [fisher] (M. pennanti), are clearly divided into two groups—the stone marten constitutes one and all the remainder; i.e. sable, pine and American martens (M. americana), even, if they are considered separate species—the other.

It is characteristic that, although in the greater part of the range of the pine marten they are encountered together (Caucasus, central and western Europe), hybrids between them are unknown, showing the generic relationships of both species. Scattered information about such hybridization, which appeared and continues to appear in the literature, has not received any confirmation. They are, apparently, based on specimens with throat patches, combining the color characters of one species and of the form of another. For example, the white patch in a form typical of the pine marten, or a yellow (yellowish) tone of the form which is characteristic of the stone marten. With the great variation in form of the patch in both species, and of its color in the pine marten, such combinations are encountered. In such cases, accurate identification is only possible from the skull.

Only one, not fully defined, case is known, of a hybrid offspring, which died immediately after its birth on a farm (Shtreili,
1932). Moreover, there is no indication about any sort of hybrid
population analogous to the *kidas*. Confirmation of the possibility
of appearance of individual hybrid animals (Shtreili, 1932 and
others) are without foundation. One of the reasons for the absence
of hybridization could be supported by essential differences in the
structure of the male sex organs (see above in corresponding places
in "Description" sections of both species).

The stone marten is a more ancient species compared to the pine marten. It is, apparently, a Pliocene form. Both species are strongly differentiated from each other by their habits and ethology (Schmidt, 1943) (V.H.).

Geographic Distribution

Found in montane regions of the Near and Middle East and Central Asia, and montane and in part plains, regions of Europe.

Geographic Range in the Soviet Union

Not extensive, constituting less than half the range of the species, and connected with the extreme west of the country and with its southern mountainous borders. Within the USSR, it is divided into several parts, isolated from each other, but united beyond our borders.

The largest—western—part of the range, which is connected with the western European part of the species range, occupies the Baltic region and includes Sarema [Saaremaa] Island (Ezel' [Oesel]) (Ognev, 1931; Kalninysh, 1950), Lithuania, parts of Byelorussia and Ukraine and several middle Russian districts. The boundaries of this part of the range are not well-understood and reliable data on them are scarce. In the north, the boundary starts at the Gulf of Finland west of Leningrad, apparently somewhere on the meridian of Chudsk Lake (the marten is known from Rakvera, the former Vezenberg), and extend southward from western Estonia, and Lithuania. It bypasses Leningrad and Pskovsk districts on the west and passes somewhere along the middle part of Byelorussia. For this part of the USSR, its range has been shown to include Grodnensk, Minsk, Brest and Gomel'sk districts (Serzhanin, 1955, 1961).

Farther, the boundary turns again, to the east in a not vet accurately established line including southern Byelorussia and Poles'ia (Gomel'sk district, Mozyr', Fedyushin, 1928; Serzhanin, 1956), passes eastward, occupying the southwestern part of Bryansk district—Surazha, Pochepa, Trubchevska, and Pogara regions (new data of A.V. Fedesov—but according to Fedosov and Nikitin, 1951. this species is not recorded in Bryansk district; Melander, 1938). It is not excluded that this marten lives in the southern parts of Mogilevsk district.

From the indicated places in Bryansk district, the range boundary goes on to Novosil' (east of Orel, former Tula governance; Ogney, 1931). In the lower Svapa, the boundary lies to the south of this line, south of Dmitriev city (Ptushenko, 1937). From Novosil, the boundary passes to Bobrov region southeast of Voronezh (Sadovoe; Ognev and Vorob'ev, 1924). South of Voronezh, the stone marten was recorded in the upper Tikhaya-Sosna and Chernaya Kalitva (Budenovsk and Ladomirovsk regions; Barabash-Nikiforov, 1957). From Bobrov, the boundary is directed to the south and then to the west in a not yet exactly established line, forming the southern border of this part of the range. It proceeds north of Lugansk, including the region to the northwest, then descends to Donetsk, and proceeds farther, somewhere in the Melitopol region or somewhat to the north, extending to Perekop or to Sivash (after Korneev, 1952). Farther to the west, the Black Sea coast forms the border.

Note. The outline of the northern and eastern boundaries of the western part of the range differs greatly from those usually presented in reports. Thus, Ognev (1931, 1947) records the existence of the stone marten in "former Pskov, Vitebsk and Smolensk governances", Yaroslavl' and Kaluga districts and believes in its "established" occurrence in Moscow district and "most probably" in the former Pereslavsk co[unty] of Vladimir governance and so on. Yurgenson (1932, 1933) describes the border of the range from Chudsk Lake to the upper Volga, and along it [river] to Zhigulei and nearly to Saratov (map), and then to Dnepropetrovsk and along the Dnepr to the Black Sea.

In the literature there are a series of precisely known occurrences of stone marten outside the above-outlined line. This line was definitely or indefinitely noted for former Yaroslavsk governance and Yaroslavl, Moscow district, Ivanovsk district, Zhigulei

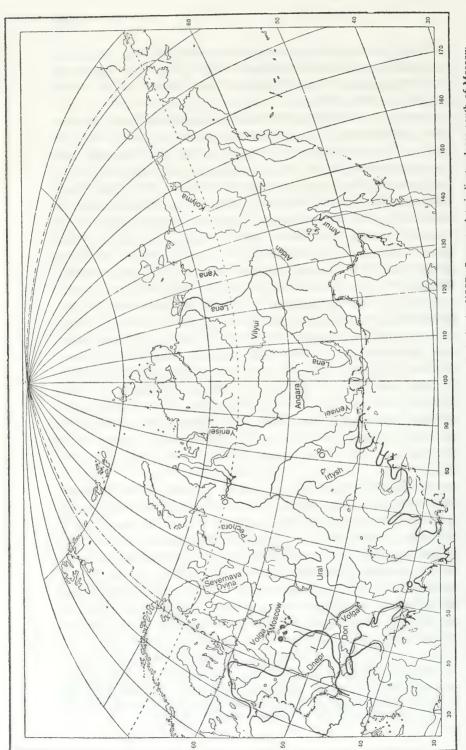
and even for the north and middle Urals, Kaslinsk Urals and Pechora-Ilych Territory (Sabaneev, 1868, 1872, 1874; Bogdanov, 1873; Varentsov, 1919, Shillinger, 1929; Ognev, 1931, 1947; Yurgenson, 1932, 1933).

Some of this information is simply fantastic. Such are data given by Sabaneev, known for his errors, for the Urals or about Pechora-Ilych Territory; information about Yaroslavl and Yaroslavsk oblast, also given by Sabaneev, did not receive any confirmation. These martens were not even observed in the Valdai Hills (Stroganov, 1934, 1936). There are no facts suggesting their existence in the former Pereslavsk county of Vladimir governance and in the Ivanovsk district and especially, in Zhigulya³⁹ and farther down along the Volga almost to Saratov. All of this information should be rejected, although on some of them, the most dubious (Urals), historical-geographical hypotheses were based.

Assumptions concerning the former Pskovsk and Vitebsk governances, if these areas are considered as corresponding to the contemporary districts, are interpreted as follows. The most westerly part of former Vitebsk governance is included in Lithuania, and the stone marten is recorded in this republic. Concerning former Pskovsk governance, in the extreme western part, which coincides with the west of present Pskovsk district, transgressions or sporadic inhabitation are possible. The above described border of the range actually passes along the border of this district. The existence of the described species in Smolensk district still is not established.

From all that has preceded, particular attention should be given to information on occurrence of the stone marten in Moscow district, along its southern outskirts and at its border. Old and poorly defined records (Sabaneev, 1872) for the district at that period were disproved (Satunin, 1892). At the beginning and middle of the 20th century, however, newer data appeared—at the Taratin quarries, near Maloyaroslavets (former Kaluga governance—hence the reference to this governance), the lake between Lukhovitsi and Stupoe, and Shchurov (Shchurov quarries) near Golutvin (Ognev, 1931, 1947; Troshin, 1961). Not all of these records were

³⁹ Bogdanov (1873) wrote: "Until now I have not succeeded in learning anything positive about the existence of the marten, *M. foina* Briss. with us (middle Volga area; V.H.). It is highly probable that it is present in "Zhigulya". Later, in literature, this careful assumption became the precedence for serious confirmation.



592 Fig. 219. Distribution borders of the stone marten, Martes (Martes) foina Erxl., in the USSR. Separate dots indicate places south of Moscow in which the occurrence of stone marten has been shown. Dotted lines outline those sections where stone martens were introduced, and later caught. V.G. Heptner.

confirmed by documented scientific material, and it is not possible to consider them confirmed. However, neither can it be fully excluded that the stone marten may rarely and sporadically be found somewhere in the Tula district (it had not been recorded there—Novosil' in the former Tula governance now lies in the present Orlov district) and, from here, individual animals may penetrate northwards to Oka and beyond. It is possible, that they dwell permanently somewhere here. Captures of stone marten in Ozeri is connected with its penetration thence from Ryazan district (Troshin, 1961), where marten was introduced for acclimatization (see below). There are no objections to this assumption.

The prior erroneous information was based either on simple mistakes (capture of pine martens with pure white patch) or on information given by poorly informed people led astray by that character. Identification of a specimen obtained from the peripheral part of the range absolutely should also be based on skull. Insufficiently critical consideration of reports on the genus led to misrepresentations in revisions (Ognev, 1931; Novikov, 1956 and particularly Yurgenson, 1933).

Some corrections to the boundary of the range of marten are possible, but at the present time, only that outlined above is reliable.

In the Crimea, the marten is widely distributed in the mountainous part of the peninsula, and is apparently not found in the plains at a distance from the mountains. Thus, the Crimean section of the range is, apparently, separated from the northern part.

The Caucasian section of the range is isolated both from the Crimean and the western parts. Its northern border passes from the lower Kuban, at first along the northern foothills of the Main Range, then proceeding as a large projection northward, including all the Stavropol uplands, and along the foothills again, extends to Makhachkala; *i.e.* the shore of the Caspian Sea. Along the valley of the Terek, the marten extends east of Grozny. Along the Caspian coast, it reaches or almost reaches the sea through the gallery forests of the Samur [river] as far as its mouth; it is encountered on the Apsheron peninsula (Heptner and Formozov, 1941; Vereshchagin, 1947, 1959). In the south, the range extends to the state boundary and beyond it. The marten is absent only in the desert plains of the eastern Transcaucasus (Vereshchagin, 1947, 1959), although, according to older data, it was met with there (Satunin, 1915).

The stone marten is present in Talysh. This area of occurrence within the USSR is, possibly, isolated from the rest of the Caucasian range.

The Middle Asian and southern Siberian parts of the range in our country are divided into a number of separate parts. In the west, the marten exists throughout the Kopet-Dag [range] down to its foot, along the Atrek [river], at least its upper course, and in the Bol'shoi Balkhan [range] (Laptev, 1934; V.G. Heptner). In southern Turkmenia, it is encountered in Gyaz'-Gyadyk (right bank of upper Tedzhen, V.G. Heptner) and in the mountainous region between Kushka and the upper Murgab (Flerov, 1932; V.G. Heptner). These are extensions of the range coming from Iran and Afghanistan.

The section of the range lying beyond the Amu-Dar'ya is quite large and includes all the mountain ranges from the Pamiro-Alaisk to the Tien Shan systems. Westward the range extends apparently along the ranges to the western extremities of the Gissar (V.G. Heptner), Zeravashan, Turkestan ranges and even to the Nuratau (Meklenburtsev, 1937). To the north, it occupies the Karatau, Talas and Kirgiz ranges and the Zailiisk Alatau, including its western spurs. Within the range are included also the northern spurs of this range, the Dzhungarsk Alatau and the small Kzyl-Togai mountains in Alakul' depression (Sludskii, 1953). The stone marten is only absent in the Eastern Pamir. Farther to the east, a section of the range occupies the Tarbagatai and Saur [mountains]. It also inhabits the Kalbinsk Altai (Kuznetsov, 1948). All of these indicated places are connected with Afghan and Central Asian regions inhabited by the stone marten.

A separate part of the range occupies southern Altai. The marten here is distributed southward to the Kurchum, Bukhtarma and Ul'ba [rivers] (Sludskii, 1953), and eastward to the frontier. The northern distributional limits in the Altai are not clear as to the accurate limits of distribution to the east. Apparently, the marten is absent at Telets Lake and along the Chulyshman (Yurgenson, 1938; V.G. Heptner). In the Sayan and in Tuva, particularly in Tanna-Ola, the marten is absent (Yanushevich, 1952).

The stone marten was introduced (59 animals in 1936) on the right bank of the Oka above the mouth of the Moksha (Ryazan district; Lavrov, 1946). This measure, naturally, failed to succeed; the marten, for 25 years, did not become a commercial species;



594 Fig. 220. Species range of the stone marten, Martes (Martes) foina Erxl. (V.G. Heptner)

however, a small number of animals were, apparently, preserved in Ryazan oblast. They spread through the northern forest past of the district, from where they had been introduced for a distance of about 100 km. From 1936 to 1952, individual cases of marten capture were known in the Kasimov region (near the place of introduction), in Gusya-Zheleznyi and Tuma regions, and near Spassk (Nazarov, 1957).

Geographic Range Outside the Soviet Union

This occupies southern and central Europe from the Mediterranean Sea westward to the Atlantic Ocean (absent in England and Ireland) and northwards to the Baltic coast, including Denmark and some islands in the Mediterranean Sea (Rhodes, Crete [Corfu]; absent on the Balearics, Sardinia, Corsica and Sicily. In Asia, the range includes Asia Minor, Syria, Palestine, montane parts of Iraq, northern and western parts of Iran, Afghanistan, Baluchistan, Chitral, Kashmir (northern), northern (montane) Punjab, Nepal, Sikkim); in China Tibet, ⁴⁰ probably Shansi and Chihli (Hebei), *i.e.* the region between the Huang He, the ocean and the Great Wall. This does not exclude the possibility that it may penetrate to the extreme southern part of northeastern China (see below).

In the north, the range is a narrow extension isolated from the previously-described Central Asiatic region, stretching eastward and occupying the montane parts of eastern Kashgariya (Tien Shan system), the western montane part of Dzhungariya (rising up to connect with the Dzhungarsk Alatau and Tarbagatai) and the northwestern and northern parts of the Mongolian Republic. Here, the range occupies, it seems, the Mongolian Altai southeastward, approximately to 100° (Ikhe-Bogdo), the Kobdo region, PriKosogol' mountains, and perhaps the Khangai.

In the literature one sometimes encounters information on the occurrence of the stone marten in northeastern China (former Manchuria; Bobrinskii, 1944 and others). This information is evidently wrong. The fact is that in the USSR, the stone marten was never recorded anywhere east of the southern Altai, or in the Mongolian Republic except where mentioned above, where it is very rare; it is not recorded in Kentei. Old information about the occurrence of the stone marten in the Mongolian Republic in the Great Khingan [mountains] (Borodovskii, 1894) and considered correct, is false (Bannikov, 1954).

Concerning northeastern China, there are no accurate and reliable data about occurrence here of any species of the genus *Martes*, except sable (series of papers, particularly in 1934 by Lukashkin;

⁴⁰No details on distribution in Tibet are known. It is very probable that it does not occupy the whole country. There is information for Kam and Nan-Shan (Ognev, 1931). The basis for confirmation of its occurrence in the Nan-Shan is not clear. Reported for Lhasa.

also in the Great Khingan according to Lukashkin and Zhernkov, 1934). The reports of Sowerby (1923), whose mistakes are recognized, are not reliable⁴¹ (see also range description of pine marten, page 846), or may be based on individual variants of Manchurian sable, the quality of which is significantly poorer than that of Siberian.

Nevertheless, the possibility that marten may appear in the extreme south of northeastern China in regions adjoining northern China is not excluded, although very doubtful. However, their very presence here (Shansi and Chihli-Hebei) calls for skepticism*. In any case, it is now generally believed that in northeastern China, at least in its northern (Great Khingan, Il'khuri-Alin') and eastern parts (eastern Manchurian mountains) martens are absent. The whole question of the existence of stone marten in China demands special analysis.

Information distributed in our literature about its occurrence in southern Finland (Ognev, 1931; Yurgenson, 1932; Novikov, 1956) is mistaken. The stone marten was nowhere in this country (Siivonen, 1956; Van den Brink, 1958).

In the zoogeographical literature, the stone marten is usually evaluated as "European", or "western" form. As seen from the outlined range, it is typically and Near- and Central Asiatic, and in part a "Western Mediterranean" species closely associated with mountains. Only, secondarily, apparently, did it settle in Europe. Its occurrence in the European plain far from the mountains, but not in other places, is apparently connected to a significant extent with humans and their constructions. In Central Europe, it is a well-marked synanthropic species (V.H.).

Geographic Variation

Geographic variation of the stone marten within the USSR is insignificant. This is related to the amplitude of racial differences, as well as the number of forms. It is highly probable, that their number

596

⁴¹This author, for example, states that "It is abundant in the western portion of the country (former Manchuria; V.H.), whence its range spreads westwards into the mountains of eastern Mongolia and on through northern Chili, Shansi and into West China. I have seen large consignments of skins, from Mukden, as well as from North Shansi, and can detect no difference between the specimens from the two regions" (p. 68)**.

^{*}Presence confirmed by Zhang et al., 1997—Sci. Ed.

^{**}In the copy I have consulted, this quote is on p. 66, paragraph 3—Sci. Ed.

is less than what is usually considered. The fur industry differentiates only two groups of stone marten: the Middle Asian, to which the martens of Middle Asia belong; and the Caucasian to which the martens of the European part of the Union and Caucasus belong. Evidently, geographic variation in that part of the range which lies outside our borders is also overestimated. The entire question needs to be reexamined with solid material.

For the territory of our country, four forms are usually considered (chiefly based on data of Kuznetsov, 1941, and also Ognev 1931; Shtreili, 1932*; Schmidt, 1943; Ryabov, 1958 and others with modifications).

1. European stone marten M. (M.) f. foina Erxleben, 1777 (syn. domestica, alba, fagorum).

General dimensions quite small, skull of average size.

In winter fur, color of back varies from quite light grayish tawny to completely dark brown. Guard hairs are tawny or chest-nut-brown, underfur is very light, pale-gray or whitish, sides a bit lighter than back and belly darker. Withers slightly lighter than back. Tail dark, brown or blackish-brown in color, darker at end. Legs dark brown. Throat patch pure white, variable in size and form.

Body length of adult males usually 450-500 mm; of females, 400-440 mm. Tail length of males—250-270 mm, of females 230-250 mm.

Condylobasal length of male skull (9) 71.0–M 82.00 \pm 0.65–84.6 mm; of females (5) 77.6–M 78.8–80.0 mm; zygomatic width of males 47.9–M 51.7 \pm 0.75–52.8 mm, of females 46.2–M 47.8–50.0 mm; height of male skull 31.0–M 31.9 \pm 0.49–32.6 mm.

Present in European part of the USSR, except Crimea.

Outside the USSR—in western Europe, except the Balkan Peninsula and Pyrenees [Iberian] Peninsula.

The marten of the part of our country mentioned belongs to the nominal form, so far as is known. Material of this form from our country, and from actual Central Europe, is very poor, and a special comparison of the East and Central European martens at a modern level has not been done. Nevertheless, the identity of these populations is sufficiently obvious.

Descriptions of fur and dimensions are based on martens of Central Europe.

^{*}Not in Lit. Cit.-Sci. Ed.

2. Crimean stone marten, M. (M.) f. rosanovi V. et E. Martino, 1917.

Dimensions somewhat smaller than in preceding form. Skull small, not massive.

597 Color of winter fur near or identical with the color of previous form. Back quite dark, smoky-tawny in color, with dark-tawny guard hairs and whitish underfur. Throat patch variable in form and size.

Body length of males 465-510 mm, of females (1) 470 mm; tail length of males 300-325 mm, of females—275 mm, length of hind foot of males 94-95 mm; height of ear of males 43-47 mm, of females—41 mm.

Condylobasal length of male skull (4) M 78 mm, of females (5) 73.2-M 75.0-76.9 mm; zygomatic width of males 42.8-M 43.8-48.1 mm, of females 42.6-M 45.7-47.0 mm.

In montane Crimea.

Outside the USSR, absent.

The Crimean form is very near to that described above, and is, apparently, identical with it (Ognev, 1931, equated the southern Ukraine marten with the Crimean form). The only difference lies in the somewhat smaller average dimensions of the Crimean martens. Beside, this was established on insufficient material. Other features given earlier (some particularities in tooth structure; Martino, 1917; Ognev, 1931) are not well-founded. The question requires re-examination.

3. Caucasian stone marten, M. (M.) f. nehringi Satunin, 1905. Dimensions large—this form is, apparently, the largest in the species within the USSR. Skull large and massive.

Winter coat quite dark, brownish-tawny or dark tawny with grayish tint, depending on effect of light-grayish or whitish underfur. Sides lighter than back, because here guard hairs are fewer and light underfur shines through more strongly. Tail and feet dark brown. Throat patch very variable in form and size, shows a tendency towards reduction.

Body length about 540 mm, tail length 250-260 mm, length of hind feet 90-100 mm.

Condylobasal length of male skull⁴² (13) 81.0-M 83.9 ± 0.29 (84.3)–86.0 mm, of females (15) 76.1-M 79.7 ± 0.69 (79.2)–82.3

⁴²Measurements of skull, as in other cases, given after Kuznetsov (1941), figures in parentheses after M—average of 20 specimens from Caucasian preserve (Ryabov, 1958).

mm; zygomatic width of the male skull 50.3-M 52.9 ± 0.47 (51.0)–56.4 mm, of females 46.2, M 48.6 ± 0.40 (44.9)–50.6 mm; height of male skull 30.1-M 32.1 ± 0.26 mm (31.7 mm)–33.1 mm, of females 29.1-M 29.7 ± 0.14 mm (28.9 mm—30.4 mm).

For dimensions of os penis, see above, "Description" section. In Caucasus.

Outside the USSR, probably present in contiguous parts of Iran and Turkey.

Differences between this form and the nominal are not sharp. Moreover, it is not clear whether the marten of the Main range and those of the southern xeric part of Trans-Caucasus are identical. There are signs of similarity between Caucasian martens and the Balkan form *bosniaca* (Kuznetsov, 1941), and of the relationship of martens of the Main range to the nominal form, and only of Trans-Caucasian, to the described form (Novikov, 1956).

4. Middle Asian stone marten, M. (M.) f. intermedia Severtzov, 1873 (syn. leucolachnea, altaica, ognevi).

General dimensions, apparently, somewhat smaller than in Caucasian form.

Color of winter fur, on average, lighter than in Caucasian marten. General tone of back grayish-tawny of moderate darkness. Sides lighter, but of same tone as back. Guard hairs dark-tawny, underfur almost white, tail dark brown; throat patch very variable, sometimes completely undefined.

Condylobasal length of male skull (5) 81.2–M 83.2–84.6 mm, of females (4) 77.7–M77.9–78.0 mm; zygomatic width of males 49.9–M 51.4–52.0 mm, of females 46.5–M 47.0–47.4 mm; height of male skull 30.5–M 31.6–32.5 mm, of females 29.8–M 30.3–31.0 mm.

In montane Middle Asia, from Kopet-Dag and Bol'shoi Balkhan to Tarbagatai and Altai.

Outside the USSR, in northern Iran (?), Afghanistan, western Pakistan, western Himalayas, Tien Shan in China, Tibet (?), and northern part of Mongolian Republic.

It is not excluded that the marten of the extreme west (Kopet-Dag) differ also from the eastern (Tien Shan); however, the distinction of the form *ognevi* was presented without adequate argument. Identity of Himalayan and Tien Shan martens is established (Pocock, 1941).

* * *

In the parts of the range lying outside the limits of the USSR, the following forms are usually recognized: 1) M. (M.) f. mediterranea Barrett-Hamilton, 1898—Pyrenees [Iberian] Peninsula; 2) M. (M.) f. bosniaca Brass, 1911—Yugoslavia; 3) M. (M.) f. milleri Festa, 1914—Island of Rhodes; 4) M. (M.) f. bunites Bate, 1906—Crete; 5) M. (M.) f. syriaca Nehring, 1902—Syria; 6) M. (M.) f. toufoeus Hodgson, 1842—Tibet, Lhasa; 7) M. (M.) f. kozlovi Ognev, 1931—Kam, eastern Tibet. The last two forms apparently are synonyms and possibly belong to intermedia (V.H.).

Biology

Population. Information is scanty. The greatest abundance of stone marten is in the Caucasus and Trans-Caucasus. In Middle Asia, they are encountered more rarely, because habitats typical for them are not found everywhere and are unevenly distributed. It is not rare in the Crimean Peninsula (V.G. Heptner), where it is met with only in the mountains. Within Ukraine, the stone marten is mainly characteristic for the territories to the west of the Dnepr, where it is primarily found in populated areas, and more rarely in forests and forest shelter-belts, and not everywhere, but sporadically. It is quite common in the forests of Belgorod district (central forest-steppe, Novikov, 1962). In the middle [forest] zone, it is a great rarity.

Habitat. The habitat of the stone marten lend themselves to division into primary and secondary. The latter appear in the plains regions of the range where the stone marten transgresses to a significant extent into populated areas, in the role of a synanthropic species. Here, it prefers to live in stone structures—in attics, cellars, sheds, stables, schools, storehouses, railway stations, in stone walls, mill weirs, and even in old stork nests, etc.

In the central forest-steppe (Belgorod district), the stone marten (Novikov, 1962) is a characteristic inhabitant of forests. It prefers old tall-trunked oak-groves on hills, especially those with broken relief. It more rarely settles in the middle-aged mixed forests or oak-groves, and avoid the sections with low relief. Here, it also settles in buildings.

Primary habitats are characteristic for those parts of the range which exhibit a more or less distinctly montane character. They are distinguished by less harsh climate; snow cover here is not

permanent and is uneven. These are unforested or almost unforested mountains, ravines, rock slides and breccias with, characteristi-599 cally, shrubby vegetation of a Mediterranean type, "maquis" or sheblvak*: forests and rocky and stony mountain slopes, deserted orchards, vineyards, and nut groves. It does not avoid montane forests, but in the Caucasus, it clearly prefers broadleaf forests in foothills. It avoids the dark coniferous forest zone, mainly because of their snowy winters. It is also encountered in rock outcrops and slides at the upper forest limits and even above, up to 2600-2700 m above sea level. In northwestern Caucasus (Ryabov, 1959), the upper limit is only 1000-1200 m. The stone marten is not adapted living in places with continuous deep snow cover. It captures food almost exclusively on the ground, hiding in the mountains, among rocks and boulders. In heavy-snow regions, marten are deprived of shelter when these regions are flooded in spring by the thaw. Moreover, they do not possess footpads densely covered with fur characteristic of sable and pine marten, and therefore are more sensitive to cold.

The weight load per 1 cm² of the supporting surface of the stone marten foot is double that of the pine marten (Ryabov, 1959): 30.9 gm and 15.2 gm; (Ryabov, this is why it obliged to avoid snowy regions).

Food. A typical feature, distinguishing the stone marten from pine marten and sable, is the abundance of plant food in its diet. In 240 feces, collected chiefly in populated places at the Pravoberezbnaya [right bank of the Dnepr] Ukraine (Pidoplichko, 1929) cherry fruits were encountered in 50%, apple and pear fruits in 25%, plums in 5%, black nightshade in 8%, tomatoes in 2.0%, mouse-like rodents only in 7%, and birds in 3%. Of 20 samples, only fruits were found in 10, and small rodents in one case. One marten ate during a winter more than 2 sacks of dry fruits in an attic. It also catches rats and mice, and rarely attacks hens.

In the forests of Nikolaevsk and Dnepropetrovsk districts (296 excrements and food items), the food composition of the stone marten was as follows (Abelentsev, 1958, % of occurrence):

Vertebrates	76.0	Plant foods	62.3
Mammals	59.0	Olive fruit	21.6
Rodents	55.6	Blackthorn fruit	19.9
Birds	44.6	Wild pear fruit	8.5

^{*}Russian word for shrubby deciduous successional vegetation—Sci. Ed.

Sparrows	34.1	Sunflower seed	11.8
Lizards	7.0	Common cherry fruit	3.5
Insects	50.0	Malagensk cherry fruit	4.5
Beetles	50.0	Mulberry fruit	4.1
Insect larvae	4.4	Rose fruit	7.4

Among vertebrate animals, the following were found:

Common wood mouse	16.2	Hares (young)	13.8
Gray hamster	14.2	Mole rat	6.0
Common vole	7.0	Spotted ground squirrel	5.4
Kurgan [barrow] mous	e 1.4	Common hamster	2.2

In summer, rodent occurrence in the food of martens reached 75-88%, and insect occurrences—75-81%. Food composition changed significantly annually, depending upon fluctuations in natural abundance of various foods.

In the "Vorskl Forest" (463 specimens; majority pertain to autumn and winter) (Novikov, 1962) rodent occurrence in various years and seasons varied from 0 to 75%; in summer from 20 to 75%, in autumn from 11 to 33%, in winter from 0 to 57.9%. The red vole was most often encountered: for the whole period, 7.3%, in summer, 16.1%; the subterranean vole—0.9%, and in summer 12.8%. Also found were water vole, the yellow-necked field mouse and house mouse, and field hare (in winter up to 1.5%).

600

The occurrence of birds in the marten diet varied in summer from 0 to 33%, in autumn—from 0 to 16.7%, in winter—from 16.6% to 88.9%. These were mainly sparrow-like birds (no fewer than 17–18 species). One litter of martens was reared on the basis of leavings from a rook's nest. Marten also eat carrion. This could partially explain the presence of poultry in food remains (Novikov, 1962). However, individual animals sometimes systematically attack domestic fowl (Ryabov, 1959). Attacks on chicken coops by marten in the Crimean preserve took place even in the presence of an excess of forest mice (V.G. Heptner). For the stone marten, birds are an attractive but difficult prey.

In summer nutrition in "Vorskl Forest", insects were usually met with in 30–66.7%. However, in the summer of 1960, they were not found at all. In autumn, their occurrence varied from 25 to 100%, in winter—from 0 to 33.3%. Among insects, beetles predominated, chiefly dung beetles captured along forest roads and paths. Overall occurrence of beetles was 22.0%.

Plant food (fruits) plays here an important role in autumn and winter. In summer, the fruits and berries occurred from 0 to 70%, in autumn—from 9.17 to 100%, and in winter—from 0 to 100% of the cases. Occurrence of sloe was 36%, pear—42.7%, and apple—17.0%. No less than 27 species of plant food were revealed. The significance of these foods in different years fluctuates greatly. Thus, in the winter of 1958, they constituted almost the only food of the stone marten. In years poor in plant yields, plant foods were completely absent in the marten's food (1947, 1962). The stone marten feeds both on carrion, as well as fruits hanging from the branches of trees and bushes.

This clearly revealed polyphagia of the stone marten usually ensures their nutritional needs even in case of sharp fluctuations in the yield of individual foods. However, in the winter of 1947, after a severe summer drought, martens were obviously hungry, feeding on garbage, feces, etc. (Novikov, 1962).

In the northwestern Caucasus, 262 yew fruits (154 g) were found in one stomach, and in the rectum—43 more. In 43 excrements collected from rock slides of the Caucasian preserve, mammals were found in 85%, birds—16.3%, of which small birds were 11.6%, and invertebrates—20.2% (Donaurov, Teplov, and Shikina, 1936).

In the Zakatalo-Nukhinsk valley (Azerbaidzhan), the food of the stone marten was composed of the following elements (Rukovskii, 1957; % of occurrence).

Mammals	65.5	Grapes	10.8
Birds	5.1	Dogwood	16.1
Reptiles	3.5	Myrobalan plum	3.5
Insects	84.0	Blackthorn	4.3
Acorns	2.4	Pear	3.5
Blackberry	23.3	Nuts	1.0

The proportion by weight of the insects and plant food here is also quite significant.

In montane Crimea, the stone marten eats grapes and grape snails (Flervov, 1929). According to analysis of 373 specimens in the Crimean preserve in 1936–1938 (M.I. Savvina) the food composition of the stone marten was as follows:

Mouse-like rodents	41.0	Molluscs	0.9
Hares	1.3	Pears	19.0

toe deer (carrion?) 1.0 Dogwood		Dogwood	7.1
Birds	16.0	Rose	9.3
Lizards	0.3	Mountain ash	0.3
Fish	0.5	Juniper	0.5
Insects	50.4	Mushrooms	1.8
Insect larvae	9.1	Conifer needles	2.0

In the mountains of Kirghizia (Kuznetsov, 1948), the stone marten eats snowcocks, partridges, raspberry and mountain ash; the latter were also observed in the mountains of Semirech'e (Shnitnikov, 1936). The old naturalists of western Europe (Brehm, 1866; Chudi, 1873) refer to rats, mice, domestic fowl, rabbits, small birds, bird eggs, lizards, frogs, bee's honey, grapes, the fruits of cherry, plum and pear, mountain ash and gooseberries, hemp seed and garden vegetables, as food items for the marten. The phytophagous nature of this animal is here confirmed.

Young martens in captivity ate in one day one ground squirrel weighing about 176 gm or 2 magpies. In two days, one marten ate a mole rat weighing 358 gm; when feeding on small animals—about 5–8 gray hamsters (weighing 35 gm each) or 9–10 yellownecked mice, weighing 20 gm each. Thus, the daily ration was about 170–250 gm of animal food (Abelentsev, 1958). In summer, a young marten ate in one day about 15 apricots whose flesh weighed about 260 gm. Upon receiving animal food, stone martens did not refuse plant food. In hot weather, they ate only mulberry fruits, cherries, etc. In captivity, plant foods were often preferred; when offered each day 10 mice and 250 g of apricot flesh for several successive days, they ate the fruits first and left the mice.

The ration for martens in the nursery [animal facility] of the Zoological Institute of the Academy of Sciences of the USSR consisted of 150–180 gm of rabbits, 25–30 gm of milk, 20–30 gm cornelian cherry or briar fruits or 30 gm boiled carrots per head. On such a ration, the martens felt quite satisfied. At the "Vorskl Forest" a stone marten ate in an open-air cage, in one day, 2–8 small birds, and moreover, willingly ate cherries and apples.

Home range. There is very little information. In one case, in the northwestern Caucasus, the area of the daily range was determined to be 400 ha and the length of the daily track was 8 km. The range was poor in food (Ryabov, 1959). In the southern Ukraine (Abelentsev, 1958), the maximum length of the marten's daily track was 5 km, but sometimes a nursing female did not go far from her

den. Tracing of 16 daily tracks in "Vorskl Forest" in Belgorodsk district showed that the average length was equal to about 1 km, rarely reaching 2.5-3.0 km.

Length of the daily track depends on the abundance of food and conditions of its availability; it is inversely proportional to the abundance and availability of food. In the starvation winter of 1946/47, martens went, in one day, over a much longer route than they did in the winter of 1957/58, when there were many small rodents and fruits (Novikov, 1962). In the first case, the average length of the daily track was 985 m, and up to 1700-2400 m, and in the second case—540 m and not more than 1100 m. The daily track may sometimes be in the form of a closed loop, but, more often, it extends in any direction. In one case, the daily range of activity had an area of about 2.5 km².

Burrows and shelters. The stone marten does not dig a burrow and does not occupy foreign ones. It prefers fissures and clefts in rocks, spaces between stones in rock slides, inhabited and uninhabited stone structures, etc. It sometimes lives in tree holes at a height up to 9 m. In the forested part of the Crimean preserve, it gives birth chiefly in tree holes (V.G. Heptner). However, in the forests of the western Caucasus, of five dens, four were in rocks (Ryaboy, 1959).

Daily activity and behavior. The daily activity rhythm in the marten is not exact. The marten is active mainly during twilight and at night, but cases of daytime activity are observed. It is a crepuscular and nocturnal animal, but to a lesser extent than the European polecat, which the marten frequently meets in one or another locality in the lowland part of its range (Shyutse, 1936)*. The marten is very active on bright moonlit nights. Being mainly a terrestrial predator, the stone marten is inferior to the pine marten in its ability to climb trees. However, it climbs well and in dense forests (Crimean preserve; V.G. Heptner), it does so frequently. It is a capable swimmer. It is active by day most often in 602 summer (Dinnik, 1914), when the nights are short. In the central forest-steppe (Belgorodsk district), the stone marten leads a crepuscular-nocturnal way of life, but in summer it is observed by day, even in midday hours. Martens living in open-air enclosures were outside at 1700-2000 hours but hid in the nest in the early morning-by 0600-0700 hours (Novikov, 1962).

^{*}Not in Lit. Cit.-Sci. Ed.



602 Fig. 221. Stone marten, *Martes (Martes) foina* Erxl, Caucasian preserve. Photograph by L.S. Ryabov and Yu.S. Danilchenko.

The stone marten captures its food mainly on the ground surface. Result from following daily tracks (Novikov, 1962) showed that along 17 km, they moved only 129 m through the tree canopy. There were 105 climbs into trees. Along the length of this route, martens examined 107 different terrestrial covers—logs, brushwood heaps, overhanging turfs, holes, root-hollows, etc. Martens also dug in the snow 34 times in open places, and near trees 23 times. For a considerable part of way stone marten went on foot, not lingering, and making only small turns. Only in thickets of shrubs, their tracks are found to meander, a characteristic for the period of fattening.

In soft snow, martens prefer to use for their movements paths of hares and ski-tracks. They rarely run along their own tracks. Martens usually move in large jumps measuring 30–40 cm in length. On firm or crusted snow or, the gait changes into small steps, and in the track, the five foot pads are well-defined. In summer, stone

martens move at a walk along forest paths and roads, and in the grass, they bound (Novikov, 1962).

Seasonal migrations and transgressions. Information is absent. Reproduction. Estrus and copulation, according to the observations of fur breeders, occur at the same time as in pine marten. In nature, individual cases of mating were observed on 18 June and 16 July. Rut in Belgorodsk district was said to take place in June ("Vorskla Forest", Novikov, 1962). Mating occurs on the ground or on the roofs of houses. It was observed early in the morning and on moonlit nights. The period of pregnancy is also the same as in pine marten, i.e. 236–237 days (Manteifel', 1947). Some fur breeders report 254–265 or 258–275 (in sable, average duration is 272 days).

The average number of young in a litter is 3–7. In individual cases 2 young were found. Parturition takes place from the end of March (22–26), to the beginning of April.

Growth, development, and molt. The young are born blind and helpless. They start to see at the age of 30–36 days. The lactation period lasts 40–45 days. Development probably proceeds almost as in the pine marten and sable. At the beginning of July (Novikov, 1962) the young are already nearly indistinguishable in size from adults. By the middle of August, a young male weighed 1032 gm, a young female, 890 gm.

Molt occurs twice, in spring and in autumn.

Enemies, diseases, parasites, mortality, competitors and population dynamics. The pine marten, and perhaps the red fox may be considered enemies of the stone marten. Large diurnal and nocturnal birds of prey, wild cats and other carnivores are a danger to the young stone marten. A case was described when a pine marten worried to death a subadult stone marten (Rimenshneider, 1920)*. Among competitors of the stone marten are the European polecat, pine marten, wild cat, domestic cat (in populated areas), and possibly other predatory animals and birds. In Germany, a case was observed when a stone marten killed a domestic cat (Kharbakh [Auerbach?], 1929)*. Also noted was a daytime attack of a stone marten on a European Polecat; the marten killed it (Frank, 1932).

Diseases are not well described. In August 1961 in "Vorskla Forest" (Novikov, 1962), two young stone martens that were obviously sick were seen: with underfur falling out and partial paralysis of the hind limbs (encephalitis?).

^{*}Not in Lit. Cit.-Sci. Ed.



603 Fig. 222. Track and scheme of bounds of the white-throated marten on soft snow. Vic. of Kislovodsk. 27 January 1950. Sketch by A.N. Formozov, about 2/3 nat. size.

In Zaporozhsk district of Ukrainian SSR, the stone marten has, in recent years, forced out the polecat, widening the region of its distribution in the southern Ukraine (Ogul'chanskii, 1954). In the Crimean preserve, a parasitic disease of the blood (theileriosis) has been observed among stone martens. Among helminthiases, the most pathogenic are crenosomatosis and mezocestoidosis of the intestines (Rukhlyadev, 1948). More than 11 helminths are known from the stone marten (Greve, 1909).

Longevity of the stone marten is not established, but is, probably, similar to that of the pine marten.

Concerning population dynamics, there are almost no data. Among the three species of the genus of true martens, genus *Martes*, it is the stone marten which most easily adapts to changes introduced into nature by humans, in some places, living together with them. In the 19th century in Germany, it was even noted that the

stone marten excludes the pine marten. After the price of the fur increased, the stone marten was subjected to intensive destruction and, hence, the question of their protection was raised.

Field characteristics. When encountered in nature, usually very briefly, it is difficult to sort out those features which distinguish the stone marten from the pine, the more so since, in some places, they are met with in similar habitats. Non-forested places or those in immediate proximity to human habitation is the best indicator that it is a stone marten. It is also said that finding the animal or its tracks among rocks and talus is another, but this indicator is less reliable.

Tracks of the stone marten are distinguished by the thinner fur covering of the foot, with well developed naked food pads (P.Yu.).

Practical Significance

The stone marten is a quite valuable fur animal, but is inferior, not only to sable, but also to pine marten. Its share in the fur market of the USSR is not great: stone marten constitute no more than 10–12% of that of processed pine marten. Its procurement is only in the Caucasus, in the montane part of Crimea, in the republics of Middle Asia and, in very small numbers, in the Ukraine. Due to the absence of more valuable colored fur in these places, it has quite essential significance in the budget of native market hunters. The experiment of introducing this animal into hunting allotments of Ryazan district (Lavrov, 1946) was not well thought out, and therefore unsuccessful. It was shown that the marten settled in villages there, living in bell towers and other buildings (Manteifel', 1947).

The stone marten is captured with jaw traps, box type traps for live capture, and various sorts of [kulemka] and plate [plashka] traps. Hunting by shooting is not efficient. Trailing with dogs, or tracking may be successful only when the animal lies up in a tree hollow. Attempts to drive the marten away from rock slides and fissured rocks is a hopeless matter. In western Europe, it is sometimes successfully shot on moonlit nights on roofs of houses in villages (P.Yu.).

Subgenus of Himalayan Martens, or Kharza

Subgenus Charronia Gray, 186543

KHARZA⁴⁴

Martes (Charronia) flavigula Boddaert, 1785

- 1785. Mustela flavigula. Boddaert. Elench. Anim. p. 88. Nepal.
- 1811. Mustela aterrima. Pallas. Zoographia Roso-asiatica, 1, p. 81. Between the Ud and Amur rivers.
- 1862. Mustela (Martes) flavigula var. borealis. Radde. Reisen Süd. Ost. Sibirien, 1, p. 19, 24. Bureinsk mountains (V.H.).

605 Diagnosis

Dimensions large—larger than all other species of genus living in Old World. Tail length considerably more than half of body length. Color bright, consisting of unique combination of areas and fields of black, white, golden-yellow and brown. Sharply outlined throat patch absent. Inner part of the upper molar only slightly larger than the outer in longitudinal diameter (V.H.).

Description

In its general appearance, the kharza is a true marten. Its typical martenness is even strengthened and emphasized particularly sharply. It is a large robust animal, muscular and flexible, with a very elongated trunk, small, pointed head on a long neck and with a long tail. Its length, together with the hairy tip, constitutes about 2/3 the body length. The tail is covered with short hairs, much thinner than in all other martens, and therefore seems even longer than it actually is. The limbs are strong and relatively short with

⁴³The proposed change of this name to *Lamprogale* Ognev, 1928 (see page 749) did not find wide application among systematists because it was not called forth from actual requirements and did not correspond with nomenclatorial rules.

⁴⁴The kharza is sometimes called yellow-cheastod or yellow-throated marten. This is an entirely bookish artificial name and the English translation is also an artificial name. In our language this name is also not preferred, because it is very similar to the forest marten—the yellow-throated—and thus leads to confusion.

broad feet—in moving, the animal strongly bends its back into a hump and moves in bounds which, at a rapid pace, are very long.

The kharza in winter pelage has relatively short fur, which does not have the fluffiness of the pine marten and sable and even of the stone marten, but it appears lean and very long—even more so than the stone marten. The ears are large—broad, but short, and are somewhat rounded at their tips. The soles of the feet are covered with hard elastic hairs; however, the digital and foot pads are completely naked and, in general, the paws are weakly furred. In short summer fur, the kharza appears still longer and thinner, with a long, thin tail.

Winter pelage differs sharply from that of our other martens in that it is relatively short, and, moreover, is harsh and lustrous, and not as dense, fluffy and compact. On the tail the hairs are short and of equal length over the whole tail. Summer fur is shorter, sparser, less compact, and not so lustrous.

The color of the kharza is entirely unique. It is bright and variegated, and is sharply differentiated from the color of the other

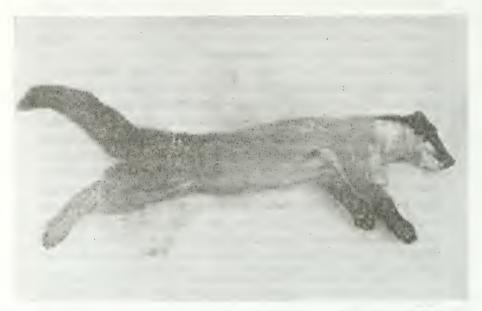


Fig. 223. Young female kharza Martes (Charronia) flavigula Bodd. "Kedrovaya" Pad preserve, southern Primorye. 18 December 1964. Photograph by A.G. Pankrat'ev.

species of the genus. The top and occiput of the head is blackishbrown with shiny brown highlights. The color of the cheeks is somewhat more reddish, which with a mixture of white hair tips produces a light gray. The posterior sides of the ears are black. their inner portions covered with yellowish-gray hairs as is the hair on the ear margin. Starting at the occiput along the dorsal surface of the body, the fur is a shiny brownish-yellow color with a golden tone. Posteriorly, this color gradually becomes browner and the rear portion of the back, and the region of the sacrum and thighs are dark-brown and blackish-brown. The sides and belly have a bright vellow tone. The chest and the lower part of the throat are still brighter than the back and belly-here, the yellow tone becomes orange-golden. The chin and lower lips are pure white in color. The hand and the lower part of the forelimbs are pure black. and the upper part of the extremities have the same color as the anterior part of the back. The transition from black color gradual. The tail has a shiny pure black color, except for the hair at the end have a light violet wash. Basally the tail hair is grayish-brown, the claws are white.

Individual variation in the fur is considerable. This concerns both intensity of general color and the color of the separate parts of the body as well as the relative development (magnitude) of the separate areas. Color of the summer fur is somewhat duller and darker—the golden tones along the back are more weakly developed. The fur of young martens is somewhat lighter than that of adults. The black tones are less pure, with a brownish mixture and the throat patch is not so bright. There is no sexual differences in color.

The skull of the kharza in general appearance, and in a series of details, is more similar to the skull of the stone marten, differing from it, most notably, in its large dimensions (see below). The brain case is relatively shorter—width between the mastoid processes is equal to, or is a little greater than the distance from the lower edge of the occipital foramen to the posterior edge of the sphenopalatine notch (ratio is reversed in stone marten). The nasal region is broader and shorter. There is no isthmus in the middle length of the nasal bones. The [postorbital] constriction of the skull behind the supraorbital process is relatively weak and is equal to the width of the interorbital space or larger. It is larger, sometimes significantly so, than the width of the skull above the canines. The auditory bullae are short and widely separated—the

distance between them constitutes about 2/3 the length of the bulla. The upper carnassial tooth is relatively large, the [upper] molar relatively small: the length of the former is greater than the transverse diameter of the latter. The inner blade of the upper molar is only slightly broadened—its longitudinal dimension is less than half the transverse diameter of the tooth. The outer lateral surface of the upper molar has a vertical groove.

The female skull is somewhat smaller than the male skull; age variation is significant, and generally corresponds to that of our other martens. The caudal skeleton is composed of 21–24 vertebrae (variation apparently, is large).

The os penis has a characteristic form and is sharply distinguished from that of our other martens. The basal half of the bone is laterally compressed from the sides and is quite tall, and is flattened below; a fissure is noticeable on the ventral side. The anterior part rises up; its end is sharply curved dorsally so that the end is directed, not forward but vertically upwards and at the extreme tip, even a little backwards. In this way, together with the extended slightly S-shape bend of the bone, it assumes a hook form. At the extreme tip, there are four small blunt processes located in the form of a corolla, each at a corner of a quadrant. These processes are directed upwards, one of them usually being larger than the others (Pocock, 1941—Indian kharza).

In all dimensions, the kharza is considerably larger than our other martens. Body length of males (9) is 500–M612–719 mm, of females (12) is 500–M575–620 mm; tail length of males (6) 370–M407–442 mm, of females (8) 354–M397.0–427 mm; length of hind foot of males (7) 100–M116.5–136 mm, of females (9) 100–M112.0–123 mm; ear height of males (4) 27–M34.5–40 mm, of females (6) 31–M37–45 mm (specimen from Ussuri Territory; Bromlei, 1956, with additions).

Condylobasal length of the male skull (8) 104–M109–112.5 mm, of females (7) 96.2–M100.6–109.4 mm; zygomatic width of males (5) 54.4–M60.7–67.9 mm, of females (5) 53.7–M57.2–59.4 mm; skull height of males (7) 38.0–M42.8–47.1 mm, of females (7) 37.0–M39.9–46.8 mm (Ognev, 1931; Bromlei, 1956; V.G. Heptner). Length of os penis about 76–78 mm.

Weight of males (eight specimens between October and January) is 2463–M3317–5748 gm, of females (10 specimens between August and February) 1155–M2765–3827 gm (Bromlei, 1956) (V.H).

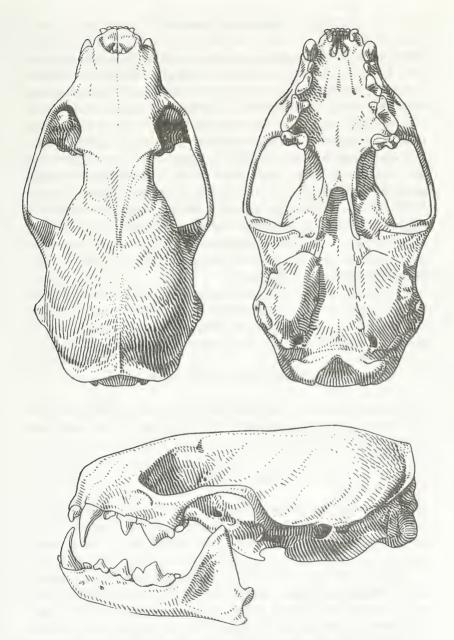


Fig. 224. Skull of kharza, Martes (Charronia) flavigula aterrima Pall.

Systematic Position

The kharza, in all respects, represents a sharply isolated species—even more sharply than the stone marten. Among Holarctic forms, according to craniological features it is, apparently, nearest to the latter. Its skull is essentially a dimensional model of the stone marten skull. Based on these characteristics its isolation from the remaining Holarctic martens is either greater or slightly greater than the stone. It is more sharply differentiated in its unique color and os penis structure. The latter character is considered by several authors as the most evident and important for species (Pocock, 1918, 1941). At the same time, it is the case that, given all of the features of similarity mentioned between all marten species, it is evidently not sufficient to separate the kharza into a separate genus. Because of the sum of characters one may consider it separable into a separate subgenus.

The kharza must be considered one of the most ancient, Pliocene forms of marten. This is supported by its peculiar range (see below). It is indicated also by the characteristic "tropical" color of kharza which is absolutely not common to all marten (V.H.).

Geographic Distribution

In forested regions of the Malayan archipelago, Indochina, the Himalayas, southern extremities of Hindustan [India], southern China and the Far East.

Geographic Range in the Soviet Union

This represents the northern border of the species range, and occupies the Ussuri Territory and the region of the middle, and in part the lower Amur. This is an insignificant part of the species range.

In the west, the northern border of the range begins (coming from northeastern China—former Manchuria) on the Amur, in the region where the Ol'doi flows into it (about 53°30′ [N. lat.] southwest of the Skovorodino railway station). At first, without noticeably separating from the Amur, orients to the middle course of the Zeya, then to the middle course of the Bureya, thence to the upper Bidzhan and Bira, including on the south in this manner, the

Burein mountains. From here, the border goes on to the middle courses of the left tributaries of the Amur—the Kur and Urmya and approaches the Amur at the mouth of the Khungarya. Along the right side of the Amur, the border passes eastward along Khungarya and, crossing the mountains, extends to the ocean in the region of the rivers Koppa, Botcha and Tumnin, crossing all of the latter. To the south of this described line, the kharza is found everywhere, noticeably increasing in numbers towards the south⁴⁵.

Evidence of the occurrence of this species between the Udoi and the Amur (Pallas, 1811)* are quite indefinite and may fully apply only to those places near the Amur. Information on the distribution of kharza in "Amur district north of the south slopes of the Yablonovyi range" (probably Stanovyi? V.H.; Ognev, 1931) 609 and even to the upper Vitim (Kashchenko, 1913), are extremely doubtful and unconfirmed, and are not taken into consideration here. At the present time, as well as in the past, even along the middle Amur the kharza is very rare (Shrenk, 1859 and Maak, 1859, do not mention it at all). It was not recorded on the Vitim in several works of the last century (Maak, 1859). It is even absent along the middle and upper Ol'doya and along the Gilyuya (Gassovskii, 1927), i.e. south of the Stanovyi range. According to the general geographical and ecological conditions, the penetration of this species far to the north is improbable. Reference to the capture of kharza in the Tuva ASSR ("Uryankhai Territory") on the Kemchik [r.] (Ognev, 1931), is completely unintelligeable and is obviously mistaken. It is also entirely absent in the Mongolian Republic. The source of these mistakes, as in the majority of similar cases, is probably imported skins.

Geographic Range outside the Soviet Union.

This occupies the eastern and northern parts of northeastern China (former Manchuria), excluding, apparently, the Great Khingan, or at least, its southern part; eastern China, including Gansu and Shensi in the west, south to Sichuan and Yunnan, with their western montane regions (eastern and southeastern edge of Tibet; the western border of the range in China is poorly known),

⁴⁵Range according to Emel'yanov, 1927; Ognev, 1931; Bromlei, 1953 and mainly according to original materials of Yu.A. Salmin and V.D. Shamykin.

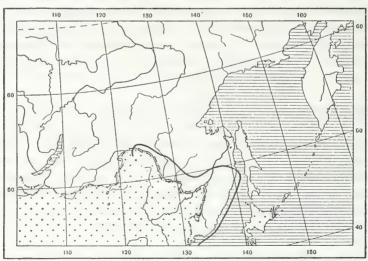
^{*}Erroneously cited as 1911 in Russian original—Sci. Ed.

Indochina with Malacca, the islands of Hainan, Taiwan, Sumatra, Banks, Java and Kalimantan (Borneo). It also occupies upper Burma and the associated Himalayan montane regions of northern India—Assam, Bhutan, Sikkim, and Nepal westward to include Kashmir, Champa, Hazara (the region northeast of Peshawar) and the Peshawar region and somewhat south of it. A separate isolated part of the range is located on the west of the southern extremity of the Hindustan [Indian] peninsula (S. Kurg, Nilgiri Hills, Travancore). Absent in Ceylon.

The range of the kharza is very typical of an eastern Asiatic Tertiary range. Apparently, the main region for the development of this species lies in the south. There is a remarkably long narrow extension of the range towards the west along the Himalayas (see range of the white-chested [Himalayan black] bear). The separated section of the range in the extreme south of India, still considered, not long ago, "unexplained" (Pocock, 1941) is typical for "Pleistocene ruptures" of ranges in southeastern Asia, manifested in past periods (V.H.).

Geographic Variation

Up to the present time, many subspecies of kharza have been described. The majority of them are groundless, and were described



609 Fig. 225. Boundary of the distribution of the kharza, Martes (Charronia) flavigula Bodd. in the USSR. V.G. Heptner.

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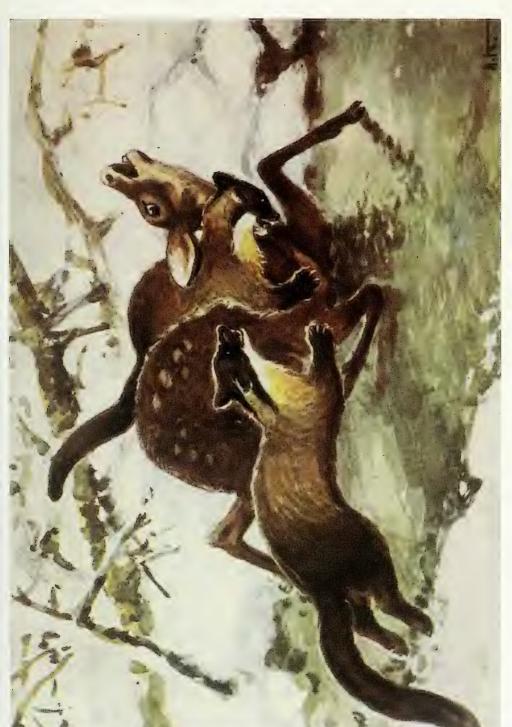
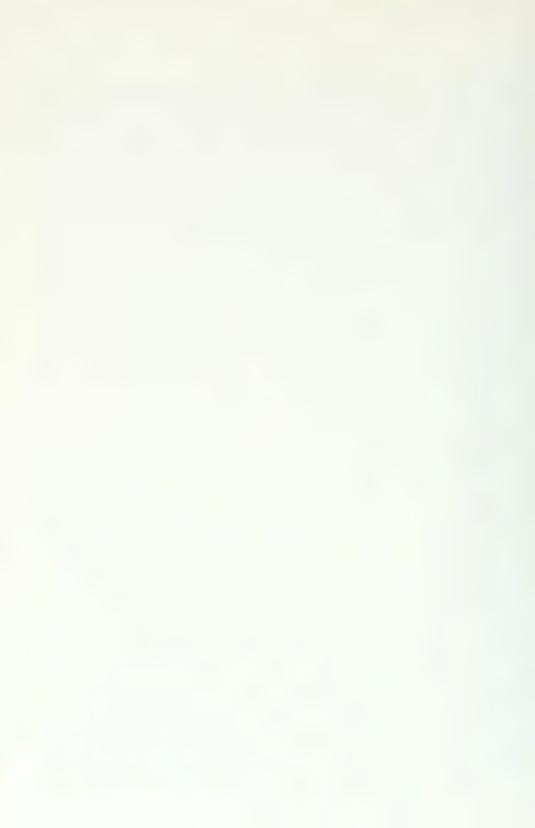


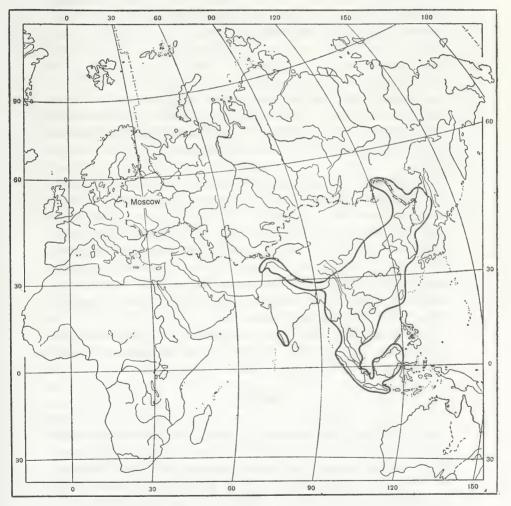
Plate 6. Kharza, Martes (Charronia) flavigula aterrima Pall., attacking a musk deer. Painting by A.N. Komarov.



on the basis of individual deviations of color or of seasonally variable characters of fur color (it was shown that summer individuals are darker).

The form existing within the boundaries of the USSR apparently, differs from the nominal (Nepal), although many authors express great doubt about this (Jacobi, 1922; G. Allen, 1938).

There is only one subspecies in our country: Amur kharza. M. (Ch.) f. aterrima Pallas, 1811 (syn. borealis).



610 Fig. 226. Species range of the kharza, Martes (Charronia) flavigula Bodd. V.G. Heptner.

It is distinguished from the nominal form by its denser and longer winter fur and somewhat larger general dimensions. For description and dimensions, see above.

In Amur and Ussuri territories.

Outside the USSR—in northeastern China (former Manchuria). The border with respect to the nominal form is not known.

Differences between our kharza and the nominal form are not sharp, but apparently are real. Body length of the latter is as follows: male (9) average —571 mm, female (9)—494 mm; tail length of males—431 mm, females—408 mm. Weight is somewhat less, apparently, and also skull (Pocock, 1941).

* * *

A series forms described in the area lying between the Himalayas and the Amur (kuatunensis, szetchuensis, yuenshanensis, melli, koreana) are completely based on information stating its similarity to the animal of the Amur form (Jacobi, 1922; G. Allen, 1938).

Outside our country, the following forms are usually accepted, 1) M. (Ch.) f. flavigula L. 1875—Himalayas, from Kashmir eastwards, southern China northward to Shensi and Gansu; 2) M. (Ch.) f. gwatkinsi Horsefield, 1851—southern India (Nilgiri Hills, Kurg, Travancore); 3) M. (Ch.) f. chrisospila Swinhoe, 1866—Taiwan; 4) M. (Ch.) f. peninsularis Bonhote, 1901—southern Tenasserim and Malacca; 5) M. (Ch.) f. indochinensis Kloss, 1916—Indochinese Peninsula, northern Tenasserim; 6) M. (Ch.) f. saba Chasen et Kloss, 1931—Kalimantan (Borneo).

Among all the listed forms, the better distinguished ones are the nominal, and *gwatkinsii*, which is usually considered to be ranked as a separate species (V.H.).

Biology

Population. Data are inadequate. Abundant on the western slope of the Sikhote-Alin', and south to the Khor and Kkhutsinka rivers. On the eastern slope, it has already become rare in the Samarga river basin (Yu.A. Salmin and V.D. Shamykin). Northward to the extreme limits of its distribution it is rare everywhere. It is

particularly numerous in the southern part of the main axis of the Sikhote-Alin' range.

In the southern part of the range in the USSR, the index of density of 3.2 per 1000 hectares (in "Kedrovaya Pad'" preserve, 1934–35; Korkeshko and Mirolyubov, 1936), is, apparently, not extreme; for this species, it corresponds to an estimation of "abundant". Figures for fur production are not indicative [of population], species is not exploited due to difficulty and unprofitability of hunting.

Habitat. Most commonly encountered in montane coniferous taiga, although in various habitats—on rocky cliffs with thickets of Mongolian oak, in the broad-leaf forest zone, in burnt-over areas, in nut pine stands, in montane spruce and spruce-fir taiga up to timberline. Most frequently, it lives throughout mossy dark coniferous forests of the Okhotsk type, along the northern slopes of the hills—in musk deer habitat—and in the valleys of rivers and streams (Bromlei, 1956). In summer, it is met with almost everywhere, appearing in great numbers in the flood plains of rivers and creeks, where it stays until late autumn. After the end of rut and spawning of the migratory fish, it becomes concentrated in montane taiga where at that time musk deer gather (Yu.A. Salmin and V.D. Shamykin).

Abroad, it occurs even in the lowland swamps of Burma and in the arid, unwooded mountains of the Northwestern Frontier region of Pakistan (Pocock, 1941).

Food. Kharza is an omnivorous animal, however, in the Ussuri Territory the foundation of its diet is musk deer, especially in the winter time. The numbers of kharza depend on their abundance. The kharza is a particular danger to the musk deer in winter time, when it is not possible for them to take the young of other hoofed animals, these are available to them only up to a weight of 10–12 kg. In autumn, it is no less dangerous for the musk deer when groups of nearly grown but not yet dispersed litters hunt musk deer. In winter, the kharza tries to drive musk deer onto the ice. In 1936 on the Armu and Nantsa rivers, over a distance of 200 km, the carcasses of 26 musk deer killed by kharzas were found (1 per 7.7 km); in 1952, along the Sitsa river—4 per 30 km. Two to three kharzas can eat a musk deer in 2–3 days (Bromlei, 1956).

Food of kharza and its seasonal characteristics are shown in Table 61 (Yu.A. Salmin and V.D. Shamykin).



Fig. 227. Montane mixed broad-leaf forests in "Kedrovaya Pad'" preserve (southern Primor'e)—habitat of kharza, and also Amur badger, spotted deer, leopard and others.

June 1958. Photograph by A.G. Pankrat'ev.

Table 61. Seasonal characteristics of diet of kharza (% occurrence)

Type of food	Entire year	Winter	Spring	Summer	Autumn
Musk and roe deer, goral, moose calves,	45.5	63.1	44.9	31.5	42.3
wapiti, wild pig (sucklin	g)				
Small exploited species	27.1	29.7	26.6	20.0	32.2
(squirrel, hare, sable,					
Siberian weasel)					
Mouse-like rodents, pika	s 5.2	_	6.1	11.6	3.4
Hazelhen	12.6	7.2	18.3	17.6	6.8
Small birds	3.4	_	4.1	7.7	1.7
Fish (migratory salmon)	2.1	_		_	8.5
Molluses	1.4	-		5.9	
Insects	0.5	*******		1.9	_
Nuts and fruits	2.2	_	_	3.8	5.1

Ungulates and small exploited animals are the main food (20% and more) of kharza throughout the whole year, and hazelhen as well in spring and summer.

Small birds, mouse-like rodents, pikas, molluscs, nuts, fruits and insects rank as secondary foods in the summer period. In autumn, fish, fruits and nuts are secondary foods of characteristic occurrence.

In the food of kharza are encountered: young wapiti, spotted deer, roe deer, goral, squirrel, Manchurian hare, white hare and flying squirrel. Mice and chipmunks are rare. Among birds, most frequent are hazelhen and pheasant. Fish, insects, molluscs and plant food occur, but are rare. In 17 data sets on diet of kharza, musk deer was found in 64% of cases, squirrel—in 18%, fish—in 18%, birds—in 11% and hazelhen—in 5.5% (Bromlei, 1956). Carrion (except fish) is not taken by kharza and it rarely returns to its prey. Captures of sable are a frequent occurrence, increasing with increase in [sable] numbers. It does not attack domestic fowl, but the old toothless individuals sometimes feed on discards.

Judging from the fact that kharza always possesses fat deposits, indicates that it is always well supplied with food and does not have a "bottleneck" period during the year.

Home range. The home range of the kharza is not permanent and is very extensive. In one day and night, it covers up to 10–20 km, moving in regular bounds, and in this way it can frequently travel around an entire river or creek basin. Usually, each 3 to 4 km, along the trail of a kharza, remains of eaten prey may be found (Bromlei, 1956).

Burrows and shelters. Information is lacking.

Daily activity and behavior. There is no information for the USSR. In India the kharza hunts by day (Pocock, 1941). It travels in pairs, but in winter, litters not yet dispersed of up to 5–7 individuals are typical. The kharza hunts hoofed animals (musk deer, roe deer) in groups surrounding the prey, as observed in India. In this way, the yield of the hunt is increased, and the hunting of this animal is determined by whether they are in pairs or a group. When hunting ungulates, it often tries to drive them onto a smooth ice surface (Yu.A. Salmin and V.D. Shamykin). In March, with weakly crusted snow, the kharza overtakes a musk deer after 800–1000 m, since the weight load of the musk deer on 1 cm² of surface is equal to 80 gm, and of kharza—only 31 gm (Bromlei, 1956).



613 Fig. 228. Habitat of kharza in "Kedrovaya Pad'" preserve (southern Primor'e). Mixed coniferous-broad-leaf forest with lianas. Photograph by A.G. Pankrat'ev.

The kharza hunts mainly on the ground surface, but climbs trees proficiently. In moving from tree to tree, it is capable of making jumps up to 8-9 m in length. In case of necessity, it jumps into the snow from the tops of the highest trees. In captivity, it is easily tamed. It is active both day and night (Bromlei, 1956).

Seasonal migrations and transgressions. After March snowfalls, when snow depth reaches 50-60 cm, the kharza sinks into the snow and prefers to move about in the tree tops, gradually descending to the montane foothills to broad-leaf forests in places with little snow.

Reproduction. Data are scarce. There are indications that the kharza is monogamous (Yu.A. Salmin and V.D. Shamykin).

Increase in activity, accompanied by signs of nuptial urges, is observed twice yearly, from the middle of February to the second decade of March, and from the end of June to the first half of August. According to other data, copulation occurs from the first days of June to the middle of July (Bromlei, 1956). At that time fights are observed among males, and the animals become unwary. Lactating females were obtained on the 4th and 7th of May. Litters contain two-three young rarely four. Young have not been observed in summer (Bromlei, 1956).

Growth, development, and molt. There is almost no information. Summer pelage of the kharza is acquired only in August, after a delayed spring molt. Autumn molt is usually not completed even by the end of September.

Enemies, diseases, parasites, mortality, competitors and population dynamics. The bold, strong and very active kharza has no enemies. Competitors are mainly those predators which feed on musk deer. Helminth infection is not large. It lives to a considerable age.

Fluctuation in numbers of kharza are closely connected with musk deer. The kharza population began to increase only in 1938, after the prohibition of musk deer trapping, which caused growth in the numbers of this ungulate. However, the population increase of kharza caused, in its turn, a decrease in numbers of musk deer. Therefore, after 1941, decrease in numbers of the musk deer, were paralleled by decrease in numbers of kharza, which, in 1946, again reached the 1938–1939 level (Yu.A. Salmin and V.D. Shamykin).

Field characteristics. The kharza is distinguished from other small carnivores of the Ussuri montane taiga by the large size of its tracks and its movement in large bounds (P.Yu.).

Practical Significance

The value of kharza as a furbearer is not great and does not compensate for the effort expended in hunting and capturing it. In the hunting industry, the kharza causes significant harm by destroying a valuable furbearer—sable. In the light of recent data on the diet of kharza, this harm is, possibly, somewhat exaggerated. It is desirable that the number of kharza be limited, but by no means achieving complete destruction of this animal, which is rare in the USSR.

The kharza is not easily trapped by snares or baited traps. The only method of capture is hunting with especially trained dogs. From 1936–1946, prepared skins in Sikhote-Alin' ranged from 42–110 (P.Yu.).

Genus of Wolverines

Genus Gulo Storr, 1780

- 1775. Gulo. Frisch Natur.-Syst. d. vierfüss, Thiere, p. 17. The International Commission on Nomenclature, has decided that Frisch's book does not satisfy nomenclatoral requirements and the names proposed in it are invalid.
- 1780. Gulo. Storr. Prodr. Meth. Mamm., p. 34, Tab. A. Mustela gulo Linnaeus, 1758.
- 615 1780. Gulo. Pallas. Spicilegia zoologica, 14, p. 25 Gulo sibiricus Pallas = Ursus gulo Linnaeus (V.H.).

Dimensions large.

Skull large and massive, broad and relatively short, with well-defined rough protuberances, crests, etc. Arrow-form (sagittal) crest high, its posterior end extending sharply backward above flat surface of occiput; occipital crest well-developed, but relatively weak. Braincase of relatively small volume. Facial part of skull short and broad (distance between margin of alveoli of middle incisors and middle of line uniting ends of supraorbital processes constitutes 65–70% of distance from this line to posterior end of sagittal crest). Nasal bones short and broad, nasal foramen large and slanting obliquely backwards in a way that makes it strongly opened upwards. Orbits relatively small. Zygomatic arches powerful and very massive, especially in posterior part, and posterior parts more widely separated. Region of interorbital constriction quite narrow (its width less than width of muzzle above canines), elongated, lateral sides almost parallel. Supraorbital processes poorly developed.

Upper profile of skull convex, considerably elevated in frontal region and thence quite abruptly depressed down to nasal region. Braincase quite narrow, but high. Infraorbital foramina small—their diameter two times less than base of upper canine. Bony auditory bullae relatively small, flattened, thick-walled and widened in transverse direction. They are slanted as regard to one another, short, with swollen inner sides; becoming wider and more

flattened towards the auditory meatus. Auditory canal well-developed. Hook-shaped processes of pterygoid bones not fused with auditory bullae. Mastoid (mammilary) processes large and protude obliquely forward anteriorly and downwards beneath the auditory meatus; paroccipital (lateral occipital) processes large, separated from bony auditory bullae. Bony palate very broad.

Dental formula as in true martens, genus Martes:

$$I\frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{1}{2} = 38.$$

First premolars sometimes absent, with socket of tooth not evident. In some cases, all four [first premolar] teeth absent. Teeth large and powerful, relatively much stronger than those of true martens (genus *Martes*). Longitudinal diameter of base of upper canine about 10 mm, usually larger (canines significantly more powerful than those of badger).

Upper molar typical marten-like in structure—elongated in transverse direction, with its inner blade a little wider than outer, but small. Upper carnassial tooth very large and strong (its longitudinal diameter exceeds that of the upper molar, by nearly four times), but the inner cusp in its anterior part is relatively weak. The main apex of this tooth is high and massive, with sharp lateral cutting edges. Lower carnassial tooth large, with two massive apices of almost equal height.

First premolars of both jaws very small and somewhat crowded into toothrow, and second lower premolar also very small, with a rounded crown. Upon closure of jaws, crowns of second and third upper and of third and fourth lower premolars do not overlap—they are located at different levels, or they only touch each other or barely come together (third and fourth)¹. The longitudinal axis of the upper carnassial tooth is parallel or almost parallel to the longitudinal axis of the skull—in all other genera represented in our country, these lines form an angle, in some quite large.

Os penis quite massive, weakly curved in the middle part, gradually thickening in basal half and thick at base. At anterior thin end, there is an expansion in form of a fist, slightly divided anteriorly.

^{&#}x27;Indications are encountered in literature that in the closed jaws the apices of the carnassial teeth (upper and lower) "are widely separated" (Ognev, 1935) were based on misunderstanding—they form tightly closed scissors.

Trunk short and massive, limbs of moderate length with large broad feet, especially in forelimbs, semiplantigrade; claws large. Facial part of head somewhat extended, eyes relatively small, ears small, short and rounded. Tail short, without terminal hairs, approximately equal to length of head. Winter fur very long, dense and shaggy, with brown tones. Seasonal dimorphism in fur character sharp, in color weak; sexual dimorphism not observed. Sexual differences in measurements quite considerable. In addition to paired anal scent gland, there are special glandular regions on the belly in front of the sexual opening, developed in both sexes². Two pairs of nipples.

The range of the genus is very large, occupying the taiga and tundra zones of both the Old and New Worlds. In the past, the range extended considerably farther to the south (for details, see below under species description).

Genus *Gulo* constitutes, within the family, one of the most peculiarly characterized genera. Its independence has never been doubted. It is a sharply characterized genus, not only morphologically, but also ecologically and zoogeographically. However, the separation of the wolverine into a separate subfamily cannot be considered well-founded. Such a point of view one would be able to hold only by admitting into consideration fine details of the entire marten family (more than 10 subfamilies), a fact (see above, family characteristics) which does not seem necessary in the systematic relationships of the family as they are described at the present time. Among the real features of the genus, it is not possible to distinguish those which, against the background of all genera, could have supergeneric significance.

Concerning systematic position, the genus is definitely closer to the true martens of the genus *Martes*. They are closely related to each other not only in dental formula and a series of features of skull structure, but also in such characteristics as the unique glandular area on the belly and a series of homologous instincts and behavioral features. On the whole, in all of their characteristics, martens stand closer to the wolverine (Krott, 1959) than to weasels and polecats, with which it is usually placed in close proximity. Only some, actually secondary features in the general appearance

²The secretion of the anal scent gland of wolverine can be smelled for a distance of 3 m. The glandular field on the belly serves to mark the territory. Of all species of the family, it is characteristic only for marten of genus *Martes*, and for wolverine.

of wolverine give an impression of great uniqueness of this form—in actually a gigantic marten (Pocock). Attempts to affiliate the wolverine with the South American *Tayra* (*Eyra*) *barbara* (Krott, 1959) are lacking in serious foundation.

The genus *Gulo* is also related to the genus *Martes* in origin. The genus is known from the lower Pleistocene of Eurasia and America (*G. schlosseri*). Its ancestor was, probably, the closely related Pliocene *Plesiogulo* (*Perunium*), known from the lower Pliocene of Eurasia (*P. monspessulanum*, *P. brachygnatus*) and the middle Pliocene in America (Simpson, 1945; Thenius and Hofer, 1960). Separation of the lineage which gave rise to contemporary *Gulo* from the genus *Martes*, which arose in the Pliocene (perhaps in the upper Miocene) occurred, evidently, in the Miocene. The genus *Gulo* itself appeared in the lower Pleistocene.

Tertiary wolverines were thermophilic, and only during the course of the Pleistocene era did the range of this group receive its recent shape—taiga and forest-tundra, and in part, even tundra.

618 Quaternary wolverines have been derived from the lower Pleistocene G. schlosseri and they do not differ from recent wolverines as regards species relationships (see below concerning distribution of wolverine outside the USSR).

In the genus there is only one species: G. gulo (Linnaeus, 1758).*

Specific identity of animals of the Old and New Worlds is evident, although several authors at the present time usually consider the wolverine of North America as an independent species (G. luscus L.³).

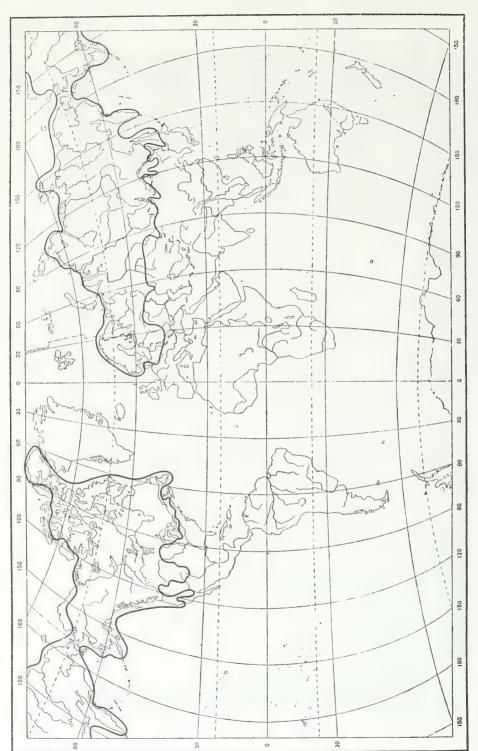
In the USSR, there is one species—the wolverine G. gulo (Linnaeus, 1758)*.

The range occupies the taiga and a considerable part of the tundra zones.

As a fur-bearing animal, of secondary importance, but is in part injurious to the hunting economy (V.H.).

^{*}Parentheses omitted in Russian original-Sci. Ed.

³The placement of the Holarctic wolverines in one species was recently convincingly shown by special investigation carried out on reliable material (Kurten and Rausch, 1959).



617 Fig. 229. Range of the wolverine genus, Gulo Storr, and species range of the wolverine, Gulo gulo L. Southern border in America greatly simplified. V.G. Heptner.

WOLVERINE [ROSOMAKHA]4

Gulo gulo (Linnaeus, 1758)*

- 1758. *Mustela gulo*. Linnaeus. Syst. Nat., ed. X, 1, p. 45. Northern Scandinavia (Lapland).
- 1780. (*Ursus*) *luscus*. Linnaeus. Syst. Nat., ed. X. 1, p. 47. North America, Hudson Bay.
- 1780. Gulo sibiricus. Pallas. Spicil. Zool. 14, p. 35, tab. 2. Upper Ob' river. Requires confirmation—Altai.
- 1792. Ursus gulo albus. Kerr. Anim. Kingd. Syst. Cat. No. 381, 190. Kamchatka.
- 1816. Gulo vulgaris. Oken. Lehrb. Naturg. 3, 2, p. 1004. Renaming of Gulo.
- 1820. *Gulo borealis*. Nilsson. Skand. Fauna. Dagg. Djur. 1, p. 95. Renaming of *Gulo*.
- 1829. Gulo arcticus. Desmarest. Mammalogie, 174. Renaming of Gulo.
- 1829. *Gulo arctos*. Kaup. Entw. Gesch. Nat. Syst. Europ. Thierw. 1, p. 68. Renaming of *Gulo*.
- 1918. *Gulo biedermanni*. Matschie. Sitz-Ber. Ges. naturf. Freunde. Berlin, p. 147. Mountains south of Telets Lake, Altai.
- 1918. Gulo wachei. Matschie. Ibidem, p. 147. Sources of Katun' river north of Belukha, Altai.
- 1922. Gulo kamtschaticus. Dybowski. Arch. Tow. Nauk. Lwow, 1, p. 349. Nomen nudum.
- 1948. Gulo gulo kamtschaticus. Averin. Trudy Kronotsk. gos. zapovednika, 1, p. 145. Nec Dybowski, 1922. Mouth of Povorotnaya river, Kamchatka.

⁴Sometimes the name of this animal [rosomakha] actually somewhat unusual, is written with a double "S" [in Russian]. At the same time, this word has nothing at all to do with the root "ross". According to Dal', this is the true name of the animal and it should be written as given above. It is also sometimes used as a word of abuse, meaning "scatter-brained, sloven", in those regions where the wolverine does not live and the people do not know it (Kursk, Ryazan, Tambovsk, former Simbirsk districts). The expression "walks like a wolverine" means to walk "wearing his clothes unbuttoned" (Dal'). The habits of this animal allows us to assume that its name has been derived from the Russian common language. In the languages of the people of Scandinavia and the northern USSR, corresponding root is absent.

Diagnosis

The only species of the genus.

Description

In general appearance, the wolverine is very distinctive, not similar to other members of the family, and is particularly strongly distinguished from the true martens and the species which are externally similar to them.

In winter fur, the wolverine is an animal of heavy, massive appearance, short and broad, especially the posterior part of the trunk, on strong short legs and very broad feet. Tail short, approximately equal to length of head. It is clothed in long shaggy hairs, weakly demarcated from the croup which is covered by dense long fur. In its general appearance, it reminds one of a bear. The head, however, is relatively small, covered with short hairs and does not appear thicker than the neck. It is moderately elongated, with small widely separated ears with rounded tips. They slightly protrude from the fur. On the whole, the head in form does not have the pointed shape characteristic of martens.



Fig. 230. Wolverine, Gulo gulo L. Sketch by A.N. Komarov.

The wolverine is a strong, clever and alert animal, but conveys the impression of being heavy and clumsy. It usually moves in jumps, somewhat laterally and as if stooping—the posterior part of the trunk is higher than the shoulder. Although all of its movements are quick, they seem clumsy and uneven, which is still more accentuated by the undulations of the long fur. In summer fur, the wolverine looks less massive but, if you like, even more clumsy. Still more striking to the eye are the thickness and strength of the legs, and the head looks much larger. In winter fur the feet are densely furred, but in summer, the naked areas on the lower surface of the feet are easily seen. Claws are light-horn, lighter at their tips; on the foreleg their length is 24–26 mm, on the hind—22–24 mm.

Pelage of the wolverine in winter is dense and long, not compactly arranged but "shaggy" and harsh. The underfur is not very dense, length 30–35 mm and not hanging down. Guard hairs are short only on the head and paws and are quite compactly arranged. Their length on the forehead is 10–15 mm, between the ears—about 52 mm, on the back—80–100 mm, and on the shoulders and thighs—120–150 mm. Therefore, the animal's trunk especially posteriorly, seems to be enveloped by a band ("skirt") of long hanging, undulating hair, imparting to the trunk in no little degree its peculiar appearance. On the legs, above the ankle and wrist articulations, the hairs have a length of 80–100 mm, and on the paws—25 mm. Body hairs weakly adhere to each other and stand at a large angle to the skin surface, marking the fur seem very fluffy. Tail hairs are extremely dense and have a length of 65–280 mm. Therefore, the tail is very thick and fluffy, although short.

The fur of wolverine is of low value due to its coarseness, but it is warm, sheds water well and is very durable—one of the most durable ("long-wearing") of furs, close in this respect to otter.¹

Summer fur is scarcer and shorter than in winter, but the relative difference in hair length on different parts of the body is retained, hair on the tail being very long and dense.

¹Apparently, therefore, guard hairs are very fluffy and the underfur does not hang down, wolverine fur in part possesses a special property which is absent in other furs: the hoar-frost from breathing which settle on it is easily shaken off and the fur does not wet. This is very appreciated by several northern people who make collars of winter clothes from wolverine fur. There, much money is paid for skins of this species. This peculiarity of wolverine fur was confirmed by investigations of the American military department, who use it for special uniform parts in the Arctic (Krott, 1959).

620

Spring molt is complete, but in autumn probably, there is no shedding (completion of hair growth). In the first autumn, the animal is fully covered with adult pelage.

The color of the wolverine is entirely species-specific. In animals of more or less average color type, the anterior part of the muzzle is dark brown. On the forehead, occupying the whole area between eyes and ears, and sometimes even descending to the zygomatic region, is situated a lighter, sometimes whitish or yellowish-white field, due to the presence of light ends of guard hairs. Ears are dark-brown, slightly lighter on the inner side. The occipital region is brown, the dorsal neck dark-brown, slightly lighter on the sides. The top of the neck, withers and the whole middle part of the back to the sacrum are occupied by a uniform color field of dark brownish or dark-chocolate color. The guard hairs have shiny dark-brown ends, the deep underfur is brownish-gray, with ashy tinges. The general tone of this "saddle" is very beautiful, deep and bright.

Extending from the sides of the neck, through the shoulder region along the sides of the trunk and further including the rump, are two light bands. They are at first narrow, not sharp and not bright, but passing posteriorly, they broaden and become lighter. They include also the hairs on the top of the proximal third or half of the tail. This pattern ("breast-band")* has a light-tawny color and is well demarcated on the general dark color of the animal. The whole lower part of the body, beginning from the chin and below the shlei, is covered with dark-brown or blackish-brown fur, darker than the saddle. Elongated white spots with irregular outlines often occur in the middle of the [ventral] neck and on the chest between the anterior limbs. The legs are covered with shiny blackish-brown hairs—they are darker than the saddle and the legs are near-black or black. The tail, except of the above-mentioned part, has a color corresponding to that of the saddle, or a somewhat lighter reddish and dirty color. In the coloration of the animals of this type, the light tones are strongly developed but cede to those occupied by dark tones.

Wolverine coloration is subject to great variation, partaking mainly an individual character, but also, although to a lesser

^{*}The Russian word "shleya" is the name for a sailor's harness that crosses the breast and over the shoulders, continuing down the sides, and is attached to rigging, enabling the sailor to haul ropes attached to the ship's rigging more efficiently—Sci. Ed.

degree, geographical (see below). This variation is demonstrated both in general color tone and in form, size and generally, degree of development of the breast-band,—deviations from the type described [above] are very great. Very dark wolverines (dark-brown in the terminology of furriers) have a very dark dark-brown saddle tone, and all remaining body parts are darker than described. The breast-band begins farther back, is narrow, and does not include, or nearly include, the tail base; colored only a little lighter than the saddle and shows weakly on the skin, mainly in the posterior part of the body. In animals of this type, the light tones are reduced both in area and in color. In extreme cases of darkening, the animal looks almost evenly colored. The frontal field is weakly defined or almost unnoticeable.

Wolverines of the light color type ("light-brown") have the saddle of light-brown color, and general tone of the remaining dark part of the skin is correspondingly light. The breast-band is well defined, distinctly observable on the broad shoulder blade, particularly posteriorly, and covers a considerable part of the tail. 621 It is light-ocherous or even whitish. The frontal transverse band is sharply defined and very light. In animals of this type, light fields are generally no less developed than dark (not considering abdomen).

In the extreme cases, the light parts of the skin occupy a very large area, and have sharp outlines and very light straw-yellow color. The dark areas are greatly reduced in extent and color—they are light, reddish-brown or brownish-red. Starting on the sides of the neck, the light stripes of the breast-bands unite between the shoulder blades, forming, in this way, a broad, completely closed ring. Since the stripes of the breast-band are very broad, the saddle itself is represented only as a small rounded dark field in the middle of the back, surrounded by a broad light area. The forehead and bridge of the nose are whitish. In this type of wolverines, the light tones exceed the dark both in extent and tone.

In dimensions the wolverine is one of the very largest species of the family. Body length of our wolverine (males and females) is 70-105 cm; tail length without terminal hairs, 18-23 cm; length of hindfoot without claws, 17-19 cm; ear height 5-6 cm; and shoulder height 35-45 cm.

Condylobasal length of the skull (old and adult, i.e. older than 1.5 years) of males is 132.7-158.0 mm, of females, 128.7-149.0

mm; zygomatic width of males, 92.7–110.0 mm, of females, 89.0–103.0 mm; interorbital width of males, 38.7–44.2 mm, of females, 35.0–42.3 mm; length of upper toothrow of males, 51.0–59.7 mm, of females, 49.0–56.8 mm. Weight in winter time is 10.7–19 kg (after Stroganov, 1962, supplemented by material from Z[oological] M[useum of] M[oscow] U[niversity] and other sources; total about 100 individuals)¹.

The measurements are subject to quite significant sexual variation—females are smaller and lighter than males, with this difference being perhaps quite significant. Some geographic variation in dimensions is present (see below).

* * *

Morphological characteristics of the wolverine are explained by Krott (1959) in his monograph of this species, by the fact that in the past as well as at present, the animal is associated with bogs. This opinion is incorrect and is explained by the fact that the author's own observations, carried out in a very limited territory in the northern part of the Scandinavian Peninsula, were mechanically extrapolated to the entire range. As is evident from the biological features of wolverine to be brought up in notes below, it has no particular connection with bogs at all. Some of the peculiar features of the animal (foot structure, fur characteristics and others) show a strong and ancient connection with snow. Also incorrect is the idea of the cited author, that the connection of this animal with bogs itself represents a known sort of biological vicariance with the wolf, which is believed to represent its antagonist. In actuality, the picture is quite the opposite—carcasses of animals rent by wolves (moose, reindeer) facilitate the winter life of wolverine. A connection of wolverine with reindeer has been noted thusly; in several places it vanishes together with the disappearance of reindeer (V.H.).

^{&#}x27;Information given in the monograph of Krott (1959); weight—20–25 kg, individual males up to 35 kg, females not more than 2/3 weight of males, often half, are incorrect. Information in our literature about 32 kg wolverines in weight (Novikov, 1956) are encountered but are doubtful to the highest degree. Even the autumn badger, heavily fattened before hibernation, are rarely more than 20 kg in weight. The American wolverine weighs 10.8–18.2 kg (24–40 pounds; Hall and Kelson, 1959). Females are less than males by 10 to 15%, but never by a third or half.

Systematic Position

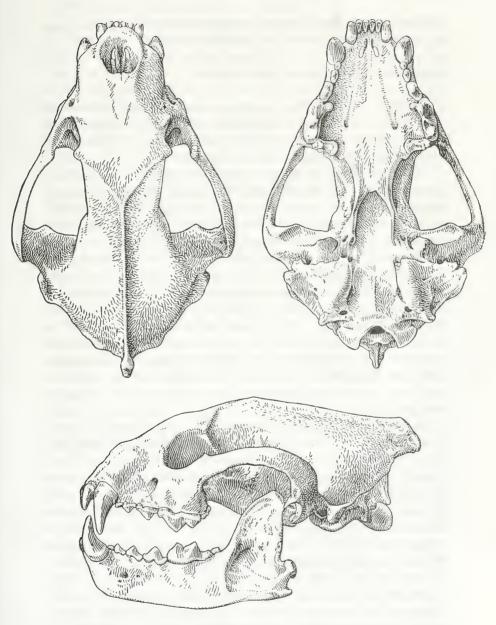


Fig. 231. Skull of the wolverine, Gulo gulo L.

623

The forest zone, mainly taiga, of Eurasia and North America, and in part the tundras of the Old and New Worlds.

Geographic Range in the Soviet Union

This is very extensive and constitutes more than half the range of the species and almost all of its Eurasian part. It occupies all of Siberia and the northern half of the European part of the Union, *i.e.* the greatest part of the State's territory.

Establishing the precise northern limit of the range is, in many cases, difficult since the wolverine roams very widely. Being, strictly speaking, a forest animal, it travels very far into the tundra, sometimes for hundreds of kilometers. Cases are known when wolverine wandered 250 km around the tundra and mountain ranges for two weeks (S. Naumov and Lavrov, 1953). In the forest-tundra, it lives a more sedentary existence and reproduces everywhere, and in several places it moves into the southern part of the tundra. At the same time, information on the distribution of wolverine and on the northern limits of its range are so very rare that it is difficult to differentiate the region of its normal and permanent existence and breeding from the region of transitory occupation. The northern border of the range given below, if not otherwise stipulated, are data on the most northerly occurrences, including transgressions.

In the west, the northern border of the range passes along the ocean coast of the Kola Peninsula (Pleske, 1886) and along the White Sea eastwards at least to the mouth of the Mezen'. At Kanin, it goes to approximately latitude 67° N. lat. (Zhitkov, 1904), but its transgression to Cape Kanin is very probable. Farther eastward, the range border passes along the shore of the Bering Sea, but in the northern tundra regions, litters are very rare, and the region of normal reproduction is, apparently, connected with the krummholz belt and perhaps with the very southern part of the tundra (Leble, 1953; V.Ya. Parovshchikov).

In the northern Ural region, the border extends to the sea (Shvarts, Pavlinin and Danilov, 1951) and includes the Yamal, passing along the Malygin Strait—(Zhitkov, 1913), therefore reaching approximately 73° N. lat. This is the extreme limit of its usual

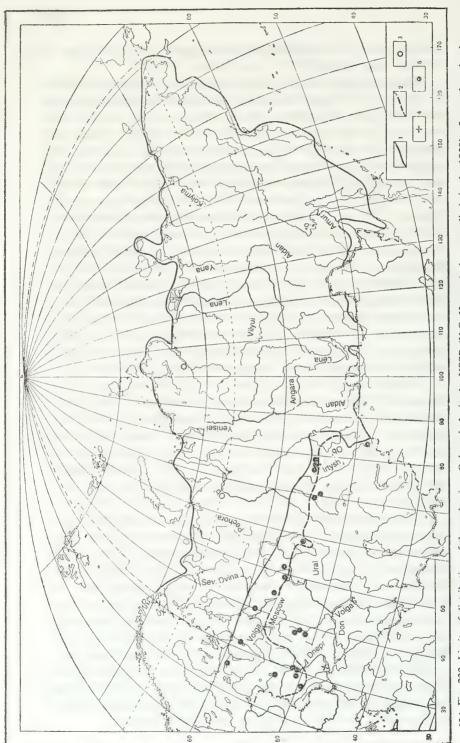
transgressions; however, a den was found in the southern Yamal at Yarro-to Lake (about 68° N. lat., Zhitkov, 1913).

Eastward, the boundary also includes the Gydansk Peninsula (S. Naumov, 1931) and, bypassing on the south the islands of this part of the Kara Sea, passes onto Taimyr. Here, the border passes very far to the north of the peninsula (north of Taimyr Lake) and nearly reaches its northern tip, probably including it entirely. The northernmost occurrences of wolverine in Taimyr are: lower Kheta and Khatanga (72° N. lat. frequently); Omuley Bay in the Yenisei Gulf at 72°40' N. lat. mouth of the Khur, left tributary of the Pyasina (73° N. lat.); Novaya and Bol'shaya Balakhnya rivers (about 73°20' N. lat.); (Yakovlev, 1930) and Taimyr Lake at 74° N. lat. or somewhat farther north. At the mouth of the Blolshaval Balakhnya it is, apparently, extirpated (V.N. Skalon). This is the most northerly place of breeding in the Old World. Finally, the wolverine was recorded (in migration) along the northeastern Taimyr coast northwards to the latitude of the Faddei islands, i.e. to 77° N. lat. or a bit to the south (E.I. Shereshevskii), and the northern extremity of Chelyuskin Peninsula (Rutilevskii, 1939). This is the northernmost occurrence of the species in the Old World.

To the east, the border passes along the ocean coast (A. Romanov, 1941) and includes the mouth of the Lena (Cape Bykov; Kolyushev, 1936) and the delta of the Yana (Bunge, 1887). The wolverine is known from the New Siberian islands—from the Bol'shoi Lyakhovsk Island (E.I. Shereshevskii) and even Novaya Siberia (Tugarinov, Smirnov and Ivanov, 1934). On the islands, the wolverine occurs only as a migrant, crossing the ice of a strait about 50 km in width.

Information on the distribution of the wolverine farther to the east, are exceptionally rare. Apparently, the boundary passes along the coast and probably reaches the mouth of the Kolyma. In all events, in this region, the wolverine lives along Omolon, and the Bol'shoi and Malyi Anyui. Beyond, the range extends over the whole basin of the Anadyr' to its mouth, including its northern tributaries, and, apparently, at least to the Chukotska (Anadyrsk) range (Portenko, 1941). The range even includes the Chukotsk Peninsula (Grinberg, 1933) and probably reaches its northern coast.

The Pacific Ocean comprises the eastern border of the range. The wolverine inhabits Sakhalin and the Shantar Islands (at least on Bol'shoi Shantar and Medvezh'e; Dul'keit, 1927) and is absent on Karaginsk, and the Commander and Kurile Islands.



of reconstructed range in West Siberia and European part of the USSR; 3-place of occurrence at mouth of Bol'shaya Balakhnya; 4-the extreme southern point of transgression (Davydov ford; 18th century); 5-individual points of occurrence (also transgression) at end of 19th 624 Fig. 232. Limits of distribution of the wolverine, Gulo gulo L. in the USSR (V.G. Heptner): 1-range limit in the 1950's; 2-southern border and in 20th century.

The outlined area of distribution of the wolverine in the south of the Far East is poorly revealed (information is partly contradictory; Ogney, 1935) and, apparently has a quite odd form. In Ussuri Territory, the range occupies the Sikhote-Alin' [range], descending along it approximately to 44° N. lat. (in Sudzukhinsk preserve, it is absent; G.F. Bromlei). This is the southernmost point of occurrence in the Old World. Thence, the border passes northward along the western slope of the range, reaching the Amur, apparently, somewhere in the region of the mouth of the Gorin. From here, it directs itself westward, across the upper parts of the Kura, Urmya and Bira, and passes to the lower Bureya and Zeya (Arsen'ev, 1923; Ognev, 1935), and somewhat to the west, exits at the boundary with northeastern China (formerly Manchuria). From the Zeva to the taiga regions of the southern Altai and Markakol Lake, the southern border of wolverine range in the USSR passes outside of the USSR or extends along its southern boundary (Tannu-Ola range; Tugarinov, 1916; Yanushevich, 1952). The animal is absent only in the steppes of eastern and western Trans-Baikal.

From Markakol Lake, the border (reconstructed), surrounding the Altai from the southwest and west, passes through the Kurchum, Zyrvanovsk, Ul'ba and Leninogorsk regions (Riddera; Sludskii, 1953), then bypasses the Tigeretsk range and then turns again to the east, enclosing the Altai from the north, and then proceeding westward and northward to the Kuznetsk Alatau and, apparently also including the Salairsk chain. From the northern portion of this range and the Novosibirsk region (Berger, 1946; Laptey, 1956), the southern border of the range suddenly turns westward and proceeds to the Urals along the band of forest-steppe through Chana Lake, Omsk and Kurgan or the region between Kurgan and Troitsk (Kurtamysh southwest of Kurgan, Talovk and Shchuch'e west of it and other places here). In the Urals, the border passes through Chelyabinsk to Zlatoust and Satka (Kirikov, 1959). Along the Ural, the range extends, southwards approximately to the latitude of Zlatoust (Sabaneev, 1874) and even to Sterlitamak (about 53°30' N. lat.; Eversmann, 1850).

In the Urals and in the European part of the Union, the range has been very greatly changed during the last century. At the same time, old information about it is very poor and the boundary of the reconstructed range might be conveyed only approximately. As with ranges of several other taiga mammals (reindeers), it is probable that they extended farther southward than at present.

The range boundary ascends abruptly northward along the western slopes of the Urals, to and somewhere near the 56° parallel, it abruptly turns again to the west, going along the Kama and Volga, seemingly to around the mouth of the Oka and farther, probably, along the more northerly part of the Oka-Volga interfluve, passing north of Moscow. It is most likely that, a very long time ago, it proceeded more southerly, i.e. included Moscow province and the entire Volga-Oka interfluve, in particular the Meshchera and several adjacent places, but in surveying that time verifiable information on the past occurrence or appearance of the wolverine, for example in Vladimir, Ryazan and Moscow districts, is absent. For the Gorkii district, there is information on the occurrence of wolverine in the past only in the northern forested parts of the former Makar'evsk and Semenovsk counties (Puzanov et al., 1955), i.e. not south of the Volga. It may be assumed that throughout the forests in the region between Moscow and the Urals, the range was local, in its southward extent, for example, along the Sura.

626

West of the Moscow meridian, the range descended significantly southward. It occupied Smolensk district, apparently, to its extreme southwestern parts, and probably included the extreme western parts of Bryansk district also (Klintsov region), Byelorussia and all the Baltic republics, including Lithuania and, probably, Kaliningrad district. The most southern place of occurrence in the west was along the right bank of the Dnepr-Belovezhsk Forest (Brinken, 1828) to the Pripyat' (Pinsk woodland), the Ovruch region (former Ovruchsk county), the Pripyat'-Usha interfluve (flowing into the Pripyat' not far from its mouth), west of Kiev near Radomyshl' (border of former Kiev and Radomyshl' counties), Kanev region (former Kanev region, i.e. near the Dnepr directly south of 50° N. lat.) and, finally, the city of Smotrich (about 40 km north of Kamenets-Podol'sk). This is the southernmost point, apparently, of the more or less permanent residence of the wolverine in the 7th cent. (about 49° N. lat.). Farther south, only transgressions were known at the end of the 18th century to Davydon Brod on the Ingulets river (100 km northeast of Nikolaev; about 47°15′ N. lat.). This is the most southern point in the European part of our country where the wolverine was recorded.

In the past, the wolverine was not encountered along the left bank of the Dnepr south of Chernigov ("Chernigovsk woodlands"—the northern forest parts of the former Chernigovsk governance).¹

As regards the extreme western parts of the Ukraine, Carpathian and Ciscarpathian, information is absent, but it is possible that very long ago, wolverine occurred in forest areas even here. The State boundary and the Baltic Sea—although the range never reaches the coast—constitute the western border of the range.

Therefore, at the southern limits of its distribution, the wolverine was also found in the forest-steppe and transgressions into the steppe zone occurred (where it still occurs at present—see below).

The range of the wolverine, and especially its southern border, was subjected to quite significant, and in some places very great, changes, during the last century. This is related to both the direct extermination and exclusion of the animal, but chiefly to the felling and thinning of the forests. At the present time the wolverine, which was also previously found in regions of broad-leaf oak-dark coniferous forests, is now restricted in its distribution to taiga coniferous forests. Therefore, the southern boundary of the range in the European part of the Union retreated northward very strongly—for more than 100 km in the extreme west, and in some places, to considerably more than the border of the corresponding zone shifted. In the east, recession was also significant, but much weaker. Moreover, in the range, which was never more or less continuous, significant "hatchways" were formed locally, associated with changes in natural conditions.

In Siberia, changes in the southern part of the range also occurred; however, they were fewer and there is very little material on them. In middle and eastern Siberia, the range, as before, reaches the State frontier, locally there are large "gaps". The southern border was also not subjected to substantive changes in the Far East. Concerning the distribution of the animal in the Altai and to its north, there are no data. In western Siberia, the southern border of more or less permanent occurrence of the wolverine in the 50's passed, apparently, along the line: Tomsk-Kozhevnikovo-Baksa river (southwest of Tomsk—upper Om'—divide between the Tartas and

¹Places of occurrence after S.V. Kirikov (1952, 1959, 1960). On S.V. Kirikov's map (1960), instead of Davydov Brod (this point is not plotted), a transgression to the Azov Sea coast south of Melitopol' was indicated. This is a clear cartographical error since in the text there is no reference of this sort.

Tara (data of Stroganov, 1962)—Tara-Tobolsk-Irbit. In the Urals, the southern border of the range passes along the line: Irbit-Egorshino-Perm' (Shvarts, Pavlinin, Danilov, 1951). Farther on, it goes a little north of Kirov, again ascends northward in the Nikol'sk region (to the Yug river south of Velikii Ustyug), goes farther to Tot'ma (at 60° N. lat.) and at approximately 60° N. lat. crosses the whole of Vologoda district. In the recent past (about 1930), the wolverine was encountered in this district and south of the mentioned parallel (Gryazovetsk region south of Vologoda; Savinov and Lobanov, 1958). To the west, the border reaches the Gulf of Finland somewhere in Leningrad district (Novikov, 1956). There have been corresponding changes on the western border of the range; northern and eastern were not affected.

The range reduction referred to took place mainly in the last century. Thus in Lithuania, Byelorussia and the northern Ukraine, the wolverine was, apparently, still a normal member of the fauna 150–200 years ago (Kirikov, 1952), and in Belovezha Forest, it was met with about 1800 (Brinken, 1828). The complete disappearance of wolverine in Byelorussia dates from the 90's of the previous century, when the last animal was killed not far from Slutsk (Fedyushin, 1929).

At the end of the 19th, and in our, century, individual observations of wolverine were known south of the described line. On one hand, they characterize the process of range reduction—the capture of the last remaining animals, as in the eastern half of the European part of the country—and on the other hand, they represent occasional long-distance transgressions of single animals. They reach not only the southern border of forests, but also the foreststeppe region and even the steppe and, in exceptional cases, the semidesert. For example, a transgression to the Kly river (north of the western tip of Zaisan Lake, in 1949, and in the 30's, of this century, semidesert) in the area north of Lake Chana (Chanov, Kuibyshev and Vengerovsk regions of Novosibirsk district, 1948-1951), to Chagly Lake north of Kokchetav¹ (1949; Sludskii, 1953, 1953a), to Borovom southeast of Kokchetay (Mikhel', 1934), to Zlatoust on the Ural (Shvarts, Pavlinin and Danilov, 1951), in the northern parts of Tatariya and to Kazan (Grinberg, 1933)2, to

¹Lake Chagly is surrounded by steppe for 10 km.

²Information on transgressions in the 20's into Ivanov and Moscow districts (Grinberg, 1933) are doubtful and are, apparently, based on cases of prepared imported skins.

Gor'kov district (1943; Puzanov et al., 1955), in different localities in Yaroslavl' district, in particular the Lyubim region, in Novgorod district (1925), to Bezenberg in Estonia (1890), in the El'tsa region on the Sosna river (1925; Ognev, 1935), to the north (Dmitryashev region; 1940) and southwest (Verkhyaya Devitsa river in Khokhol'sk region; 1952) of Voronezh (Barabash-Nikiforov, 1957), to the Slutsk region in Byelorussia (see above), in the northern parts of Kiev district and to Kiev, in Radomyshlya (1914) and Proskurov (1924; Sharleman', 1952)* regions and a series of others.

Geographic Range outside the Soviet Union (see map in genus description)

In North America extends to the northern shore of the continent (except, apparently, a narrow strip of the Arctic coast of Alaska) and occupies the entire Arctic archipelago, including Ellesmereland (the northernmost point of the species range as a whole—north of 80° N. lat.), except for Banks, Prince Patrick, Sverdrup and several others in the northeastern part of the archipelago (Hilzheimer, 1930); the wolverine is absent in Greenland.

The southern border goes through New Brunswick, Maine Vermont, New York, Pennsylvania, northern Ohio, with an extension to the south into southern Indiana and thence passes to the northwest to northern Minnesota and North Dakota. From here and as far as the Pacific Ocean, the range passes far to the south in the montane regions as large extensions. One narrow extension passes from North Dakota and Montana to western Nebraska; another from Montana and Idaho as an extension of complicated outlines extending, in a divided manner, to Utah and Colorado; a third, inclining toward the coast of the Pacific Ocean, passes at first along the western parts of Washington, Oregon and northwestern California and then, as a long extension, along the Sierra Nevada almost to 35° N. lat., or a little to the south. This is the most southern point of occurrence of the species. The range includes Kodiak, Vancouver and several other Canadian islands in the Pacific Ocean. On the Atlantic coast, the range occupies Newfoundland, but Anticosti, Prince Edward and Queen Charlotte Islands** are not included in the range.

^{*}Not in Lit. Cit.-Sci. Ed.

^{**}These are off the Pacific, not the Atlantic, coast-Sci. Ed.

In the Old World, the reconstructed range occupies the Scandinavian Peninsula (in the extreme south, transgressions occur in recent times), Finland (at present, absent in the southwestern part), and central Europe to Braunschweig and Saxony and to Poland (in the mainland of Europe, it has been absent for a long time). In Asia, outside the limits of USSR, the range extends southwards to the northern part of the Mongolian Republic. In northeastern China (former Manchuria), the range occupies the Great Khingan (probably, its northern part) and Ilkhuri-Alin mountains (Baikov, 1915; Lukashkin and Zhernakov, 1943). Its occurrence in Lesser Khingan was recorded (Baikov, 1915). In the Mongolian Republic the range occupies Kentei down to Ulan Bator and even a little to the south (about 47°45′ N. lat.) and the PriKosogol' mountains.

In the Pleistocene and Holocene, the wolverine was found outside the region of occurrence outlined above; in historical times it was encountered in Poltav and Voronezh districts, in the Crimea, in the Caucasus (Trans-Caucasus), in Hungary, Czechoslovakia, Poland; German Democratic Republic and Federal Republic of Germany, Italy, Belgium and England, France, Switzerland, Austria, and Rumania (Pidoplichko, 1951; Krott, 1959) (V.H.).

Geographic Variation

The wolverine is referred to as one of the few mammalian species in which, with a vast range, reveal insignificant geographic variation. This variation bears a clinal character, and in the Old World, differences are expressed not so much in variation in meristic features or qualitative structural differences of the skull as in color variation. Geographic variation of this character is expressed in the lightening of color from west to east. This lightening occurs, however, not by means of gradual lightening from one population to another, but through changes in relative constituents of the separate color types described above, and of intermediate between them. In this way, wolverines in the west are darker—"dark-brownish" prevails, while others are found in which the breast-band is almost undeveloped and extremely light *i.e.* "light-brownish" are few; those in which the saddle is in the form of a small spot are completely absent or extremely rare. In the extreme east, the picture is the

reverse, and in the whole intervening extent is a region where, an increase in number of light variants is observed. In general, geographic variation of wolverine, in particular the ratio of colored types in different populations, is poorly studied.

Within the boundaries of our country, it is possible without doubt to distinguish 2 extreme forms. Probably, a third—intermediate—type may also be distinguished.

1. European wolverine, G. g. gulo Linnaeus, 1758. (syn. vulgaris, borealis, arcticus, arctos).

Dimensions relatively small.

Dark and very dark individuals predominate in population. Breast-band not broad, dark or moderate color intensity. Its anterior ends do not unite on shoulders. Light individuals absent or rare.

Condylobasal length of male skull 132.7–151.3 mm, of females, 128.7–148.2 mm; zygomatic arch of males, 92.7–110.0 mm, of females, 89.0–100.0 mm; interorbital width of males, 38.7–43.0 mm, of females, 35.0–42.0 mm*; length of upper toothrow of males, 51.0–56.3 mm, of females, 49.0 to 52.0 mm (Stroganov, 1962).

European part of country and in West Siberia. Borders in relation to following form unknown.

Outside the USSR-Scandinavian peninsula.

2. East Siberian wolverine, G. g. sibiricus Pallas, 1780 (syn. biedermanni, wachei).

Dimensions as in preceding form.

Dark individuals and those of moderate color intensity predominate in population. Light forms occur more often than in west. Breast-band quite broad and light. Extreme light individuals absent or rare.

Eastern Siberia and Far East, except region occupied by following form. Borders in relation to both other forms not clear.

Outside the USSR—in the northern part of Mongolian Republic and northeastern China (former Manchuria).

Note: This form is conditionally given here for the first time. Possibly it is identical with the European which, however, is doubtful.

The name given by Pallas (1780) may possibly not belong to the East Siberian wolverine. If the type locality of the name *sibiricus*

629

^{*}In Russian original, erroneously given as "89.0 to 93.0"-Sci. Ed.

is considered 'upper Ob'' i.e. Altai, then it is not excluded that it belongs in the synonymy of the nominal race, since it is possible that it, and not the eastern form, lives in Altai. In order not to create new names, it probably is rational to transpose the type locality of the form *sibiricus* to the east (for example, Cis-Baikal). In any case, the names by Matchie as synonyms are related to the Pallas name.

3. Kamchatka wolverine, G. g. albus Kerr, 1792 (syn. kamtschaticus Dyb., kamtschaticus Averin).

Dimension on average somewhat greater than in European form. Light and very light individuals predominate in population. Anterior ends of breast-band usually unite on shoulders, and whole band forms closed ring. Breech-band is light, often so broad that saddle is in form of small dark spot which is completely surrounded by light area of breast-band. Color of breast-band often light strawyellow and whitish or almost dirty white.

Condylobasal length in males is 146.0–158.0 mm, of females, 142.0–149.0 mm; zygomatic width in males, 101.0–108.0 mm, of females, 98.0–103.0 mm; interorbital width in males, 41.9–44.2 mm, of females, 98.0–103.0 mm; length of upper toothrow in males, 54.5–59.7 mm, of females, 54.2–56.8 mm (ZMMU and Stroganov, 1956).

Found in Kamchatka and extreme northeastern Siberia (Anadyı Territory, Chukotsk and Koryakland).

Absent outside the USSR.

The details of the distribution of this form, the range of which is, probably, not restricted to the above-mentioned part of the northeastern extremities of Asia, and its limits to the west and south, are still unknown. The wolverine of the southern part of the Far East is darker, and seems not to be attributable to it. The Kamchatka form is a well-defined subspecies.

* * *

In America until recently, the existence of one wolverine species with four subspecies has been accepted (*luscus*, *katschemakensis*, *luteus*, *vancouverensis*; Hall and Kelson, 1959). However, a special study showed (Kurtén and Rausch, 1959) that this Eurasian species is represented by one form only, *G. g. luscus* Linnaeus, 1758.

It is primarily that the American form, craniologically well differentiated from the contemporary European one, is very similar, apparently identical, with the form of the European Pleistocene. Evidently, the rate of evolution of the Eurasian wolverine was more intensive than that of the American (V.H.).

Biology

Population. The wolverine is a rare animal, never forming high densities anywhere. Indications of its relative numbers are supplied by information on prepared skins of hides: 70% of the catch—Siberia and Far East, 20%—Urals and 10%—European North.

However, the quantity of skins is a poor indicator; capturing this animal is difficult and sporadic. The typical density (per 100 hectares [= 1 km²]) of the wolverine in regions where this animal is common, fluctuates between 0.007 and 0.22. Densities of about 0.1–0.2 always are associated with high concentrations of ungulates. In British Columbia, 0.07 wolverine tracks were found per 10 km of route (Quick, 1953). One wolverine was caught on average in each 3.58 km² (MacTaggert Cowan, 1957). In Sweden and Lapland (forest), the natural density in area with low yield of food was 0.01 [per km²] (two wolverines per 200 thousand hectares) (Krott, 1959).

On the basis of approximate calculations of density and areas, the number of wolverines in the USSR may be determined as 7,000–7,500 individuals.

Habitat. The wolverine is widely distributed within the confines of coniferous taiga and forest-tundra. It also enters the open tundra, but here it is rare. It much more rarely penetrates into the zone of the mixed forests and to the West Siberian forest-steppe.

It is encountered both in the plains and in montane conditions. Toward its landscape surroundings, it is quite undemanding, although it has been noted that it is somewhat attracted to marshy areas (Krott, 1959). Deep snow cover usually provides the wolverine with an advantage in following its prey, and, therefore, the main part of its range lies within the boundaries of deep snow; 50–70 cm and more; however it is not restricted therein. The winter period of deep snow (February–April) is particularly favorable to it (Teplov, 1955). The duration of the snowy period (220–240 days) may also be considered a favorable factor (Krott, 1959).

In summer, a time of more food security, the wolverine lives in very different habitats. Before the young become independent, the females are, probably, considerably less mobile than in winter and do not go far from the den.

In winter, and in the period of calving of ungulates, the wolverine confines itself to the region of their concentration. In Altai, wolverine avoids human settlements. In Lapland, however, dens with litters located 2.5 km from a village have been noted (Krott, 1959).

Food. The food composition of wolverine is essentially different in snowy and snowless periods of the year, a fact which was established in several free-living tame animals (Krott, 1959). In spring, they very intensively searched for and successfully obtained egg clutches of ground-nesting birds and destroyed them in great quantities. These were more often the clutches of ducks and other birds, and considerably more rarely, those of tetraonids (from 1948–1956, there were only 6 cases); this, apparently, was explained by the difficulty the wolverines had in finding them. They also did not destroy the crane nests found in their area of activity.

The larvae of wasps are of great importance in the nutrition of wolverines in summer. With the ripening of fruits, they give greater attention to cloudberry, raspberry, blueberry, cowberry, cranberry and crowberry. They rarely eat bog billberry. The wolverine prefers bird eggs, berries and wasp larvae to mouse-like rodents. The latter become, in "lemming" years, of great significance in the Scandinavian Peninsula. Cases of wolverine feeding on fish, amphibians, reptiles and crawfishes have not been noted; however, on the Pechora, it feeds on the carcasses of spawned-out salmonids cast up on the bank. It is only rarely that, in the snowless period, it hunts hazelhen, capercaillie and white hares. The young animals do not pursue forest game. They prefer carrion to fresh meat in summer. In summer, the wolverine does not attack ungulates and small domesticated livestock, or does so very rarely (Krott, 1959).

Ungulates everywhere constitute the basis of winter nutrition of wolverine, which is fairly well studied. Most frequently, these are reindeer and elk. In the montane taiga of Siberia, evidently they locally become musk deer, maral and Manchurian wapiti, roe deer and Siberian ibex. In the Altai (Dul'keit, 1953), in Lapland (Nasimovich, 1948; Semenov-Tyan-Shanskii, 1948) and in other places, the wolverine feeds on ungulates mainly in the form of

carrion. Within the Altai preserve, carrion constitutes 66.7% of occurrences. In Pechora preserve (Teplov, 1955), with elk and reindeer numerous, feeding on live animals is much more frequent.

631 All ungulates in the food of wolverine constitute from 45 to 75% of occurrences. Everywhere, the victims of wolverine are, first of all, those weakened from various causes, diseased and injured animals as well as juveniles. Reindeer become its victims notably more often than elk. Among the latter, the young more frequently die (Teplov, 1955). The share of carrion sharply increases with the appearance in regions inhabited by wolverine, of wolves and with increase in their activity (Nasimovich, 1948). In the absence of the latter together with scarcity of ungulates, as well as in summer, the role of ungulates considerably decreases and the basic foods (20% occurrence and higher) become white hares, tetraonid birds, forest voles, and in some places nut pine "nutlets". Among those foods of secondary importance are the squirrel, flying squirrel, fox and others, which are usually rarely utilized in the diet. It is not a rare event when the wolverine attacks as prey the weaker predators otters, pine martens and foxes. The latter are most often attacked in lairs while sleeping, sometimes near carrion. Not rarely, wolverine utilize the food remains of not only wolf, but also brown bear (Lapland) and also lynx (Dul'keit, 1953; Teplov, 1955). In Norwegian Lapland, in April 1951, remains of white hare, reindeer and willow ptarmigan occurred in a snow burrow where were found a litter of wolverines (Boehm, 1953).

Wolverine, systematically though not often, rob the traps of hunters eating the bait and the catch. When possible, the wolverine plunders stocks in the hunter's hut. In rare cases, it eats fish—at the expense of the river otter's catch, and getting the dead fish thrown on the bank.

The wolverine's stomach can hold up to 2 kg of meat, constituting about 17% of its live weight. It was, however, shown that feeding once a day, wolverine cannot eat more than 800–850 g, this is actually the maximum weight of its stomach content, i.e. it does not consume the maximum volume of its stomach (Teplov, 1955). Therefore, current opinion about the voracity of this animal is not justified. Even with abundant food, the wolverine does not eat "to satiety", and makes significant stores by pulling off pieces of meat and hiding them in the snow or at a tree in an area of up to 10 hectares around the animal carcass. Even in Pechora, where

the wolverine has a good supply of food and is often distinguished by being well-nourished, it does not eat each day: from data on 12 daily tracks of wolverine, this was noticed in 7 cases (Teplov, 1955).

Home range. Observations in nature during the course of several years on tame free-living wolverines in Sweden and Finnish Lapland (Krott, 1959) showed that each wolverine separating from its litter, takes over a vast, but quite definite home range or hunting territory. Within its boundaries it leaves its scent marks on logs, stones and other noticeable places (urine, secretions of the precaudal and abdominal glands). Between home ranges, there are no neutral zones. Therefore, despite very great daily movement, the wolverine is not nomadic, but is a settled animal. In Swedish Lapland, one male lived within its hunting territory for a period of not less than six years.

The area of such a hunting territory in the places with little food is very great—from 200–300 to 1000–1600 km². In Swedish Lapland, the area of the hunting territory of an adult male was about 2000 km². Exploring females occupied a hunting territory with an area 400–500 and 400–450 km², and an exploring young male—700 km². In areas with greater food, rich in ungulates and tetraonid birds in Finnish Lapland, the hunting territories of wolverines were smaller—about 300 km² for females and maximum distance between brood dens—an average of about 20 km. In British Columbia, the home range of wolverines equaled 124–132 km² (Quick, 1953).

The dimensions of the hunting territory, therefore, are variable and depend on a series of features at the given locality. On the other hand, the structure of the wolverine hunting territory is very stable—a large hunting territory for a male includes 2–3 smaller female territories.

Wolverines usually do not transgress on foreign hunting territories. On penetrating a foreign hunting territory, they are actively pursued and driven away, and fights occur between males. This aggression is characteristic of adult males and does not extend to females (Krott, 1959). With predominance of carrion feeding, the exclusivity of separate hunting territories is smoothed out. In several days large carrion sometimes attracts to it several wolverines (for example, 3 wolverines in 25 km²). It is possible that this occurs among animals from one litter (cases were noted when the litter remains with the mother for the winter) or a group forming a structural population unit (1 male, 2–3 females).

Using for the most part one and the same routes, often by its own old tracks, the wolverine periodically visits the particular parts of its territory. In winter, these are mainly places of elk concentration, the winter pastures of reindeer, etc.

Burrows and shelters. In winter, the wolverine has no permanent shelter. Its lairs usually occur under the protection of the spruce crowns bent down low, and more rarely on hidden elevated places. The animal prefers for its lair the places without an open approach. On the Pechora, in the severe frosts, the wolverine hides in semiburrows in the snow. The dimensions of the lair are usually about 40×55 cm.

For its litter of young, the wolverine makes a den differently: in a shallow ground burrow, under a twisted, downfallen tree or directly in the snow under dry logs in a snow depth of about 1.5 m. Sometimes, in such a den, it makes a deep path in the snow, in other cases, the lair is protected from above only by the trunk of the fallen tree. The nest itself may be lined with dry fur and grass or branches of spruce and fir. In montane localities or on the seashore, wolverine makes the brood den usually in a crevice among rocks or in the small caves in the very isolated places which are difficult to reach. In April 1951, a litter of three young wolverines was found in Norwegian Lapland, in a snow den. The nest chamber was located 20 m from the entrance to the den.

Daily activity and behavior. In the upper Pechora, the wolverine is mainly a nocturnal animal. Only in spring (March-April), *i.e.* in the period of nursing the young, diurnal activity is observed more often—up to 75% of observations—while in the winter months, 25% (Teplov, 1955).

In winter, in Lapland preserve, it is active in the period of polar night mainly during the day (Nasimovich, 1948); the observations carried out for several years in the Scandinavian Peninsula (Krott, 1959) led to the conclusion that a definite diel rhythm of activity for the wolverine is absent.

Wolverine obtains its food by thoroughly concealing itself from its victims, by extended pursuit, by ambush (sometimes from tree branches), taking away the prey of other predators, eating the remains of their meals, and carrion. It waits for hare on the paths and attacks tetraonid birds while they are resting, in mating places and in snow holes. In searching for food, wolverine seeks out the tracks of fox, lynx and others, but it avoids walking along wolf tracks. In

pestilence years, wolverine search out and eat carcasses of small animals—hares, squirrels and others. In its winter diel pattern it conducts its movements in a straightline fashion, mainly between concentrations of ungulates. These movements constitute up to 54% of its daily activity.

In searching for food and while fattening, its path is usually twisting. While walking, the animal examines large trees and the hollows in them, and looks under logs and stones. It willingly uses the old tracks of elk and ski-tracks of hunters to assist its movements on deep soft snow. In Sweden and Finnish Lapland, wolverines usually periodically examine their vast hunting territory covering a circle of about 1 km diameter. The outlines of the daily movement in these places usually have a serpentine appearance, with wide loops. Tracking a wolverine there is very difficult, particularly if it is followed, since it prefers to walk through "strong", difficult of access, places (Krott, 1959).

The wolverine is a very active animal and has great endurance. During a winter diel period it moves from 8 to 45 km, averaging 21 km, but this is not the maximum figure (Nasimovich, 1948; Teplov, 1955). In British Columbia, a wolverine traveled in one day about 32 km in one direction. In Swedish Lapland, an 8-month old male once went 34 km during the night. Following prey, a wolverine may move a distance of about 50 km. A case was also recorded when an adult male went 70 km without rest (Krott, 1959).

The wolverine is well adapted to snow cover—the weight load on 1 cm² of its foot (Teplov, 1955) ranges from 19.5 to 29.0 gm, averaging 22 gm, and according to other data (Dul'keit, 1953), 27–35 gm.

It climbs trees quite well, sometimes descending head downwards, but it never jumps from one tree to another (Krott, 1959). Unsuccessful hunts constitute a common phenomenon for wolverine, especially when pursuing ungulates.

Seasonal migrations and transgressions. Regular migrations are unknown in the wolverine. Rare cases of the wolverine's appearance in the belt of mixed forests, in the forest-steppe of West Siberia (Vengerovsk and Kuibyshevsk regions of Novosibirsk district) and even in pine forests in the Kokchetav steppe, may in some measure be related to its eviction beyond the limits of its range (Sludskii, 1953). Movements for a distance of 250 km are

known for separate individuals (Naumov and Lavrov, 1948). In years past, the appearance of wolverines in the Baltic region—Latvia and Estonia—were noted (Kh.I. Ling).

Reproduction. In Pechora preserve, signs of estrus and mating do not occur in the period from October to May. Apparently, they take place in the period June-September (Teploy, 1955). In Moscow Zoo, signs of sexual excitement were observed in June-July (Manteifel', 1947). In Pechora, parturition proceeds in the last days of February and in the beginning of March; on Kola Peninsula (Nasimovich, 1948)—in April and the beginning of May, Therefore, the time of birth of the young for example, extends for two months, and pregnancy has a latent period. The investigations of wolverine reproduction carried out in Alaska (Wright and Rausch, 1955) on material from 22 males and 11 females during the period from 1950-1953, showed that in the October-December period, only unimplanted blastocysts were observed, and in the ovaries inactive corpora lutea, the fact of migration of blastocysts from one horn of the uterus to the other was established. In January and the beginning of February, only implanted embryos and active corpora lutea were detected. In April, females revealed signs of lactation and placental scars in the uteri were observed. It was found that in males, testes and their accessories [glands] begin to function at the beginning of February, but activity, with sperms in the accessories was only from the beginning of April. Therefore, in Alaska the breeding period extends from April to October; copulation immediately after parturition, as in the polecat, is physiologically impossible.

Observations from foreign zoos in various years showed that copulation (lasting up to 30 minutes) has a local, variable form—the end of April, the end of May and the end of June (Krott, 1959).

In Pechora, the time of birth of the young is the last days of February—the beginning of March; in the Scandinavian Peninsula, a litter found in February was demonstrated (Boehm, 1953). According to data from 13 litters from Sweden and Finland, within February–March, the age of the separate litters may differ by several weeks. The earliest case of parturition was on 11 February (Krott, 1959).

A female having offspring remains barren the following year; i.e. barrenness in adult females is not less than 50%. This also occurred in cases when hunters take the litter from her. At Pechora,

the percentage of barren females is more than 60%. In Copenhagen Zoo, a female gave birth to offspring in two successive years (Wright and Rausch, 1955), which may be explained by conditions pertaining to captivity with a year round abundance of food.

The litter usually comprises 2–3 young, rarely four. Out of 13 cases, in 10 there were two young each, and in three—3 cubs each. Out of 38 cases, litters of three occurred 17 times, two—18 times, four—2 times, and one—1 time (Krott, 1959). Average litter size in the Scandinavian Peninsula is 2.5. In Pechora, according to data from 7 litters, most often 2 young occur (Teplov, 1955).

In Alaska, judging from limited material (7 females), wolverine fertility was apparently higher, there were four corpora lutea in six cases and 5 in one. Parallel to them, there were 4 and 3 placental scars, 3 and 4 embryos, and [an average of] 4.4 and 2 blastocysts. Therefore the average number was revealed as 3.4; at the same time the difference in the number of corpora lutea shows an embryonic mortality equal to 17%; moreover, dead and resorbing embryos were observed.

Besides the main den (see above), the female earlier prepares several reserve lairs, to which it transfers the litter in case of danger. The male never approaches the litter's place (Krott, 1959).

In tamed animals, the first estrus was in three-year old females, but without subsequent pregnancy. Complete sexual maturity appears simultaneously in both sexes at the age of four years (Krott, 1959). In Alaska, sexual maturity of wolverine begins, apparently, at the age of two years. Among immature males, it was impossible to distinguish morphologically more than one age class. They are easily differentiated from those sexually mature by the dimensions of the baculum (in ermine, the growth of the latter character is due to effect of sex hormones; Wright, 1950). At the same time, the growth and development of the skull of male young wolverines take place very quickly—in the course of the first year of life (Wright and Rausch, 1955).

Data on the sex ratio in the population and the rate of mortality in it are almost absent, and, hence, there are no data on its annual growth rate. In Alaska, one female, in February, had among 4 embryos, 2 males and 2 females (1:1). Among 22 captured males, 9 were adult and 13 were young; among 11 females—7 adults and 4 young, *i.e.* adult animals constituted 48% and young—52% (Wright and Rausch, 1955). Deriving from 3.4 corpora lutea per

adult female, the potential growth must be 75.5%, and embryonic and postembryonic mortality—23.5%. Barrenness in adult females (50–60%) lowers the calculated population growth two-fold, to 33%, and taking into account calculation of mortality—to 25.2%.

Growth, development, and molt. The weight of embryos several days before parturition equals 73 (o'o)—83 gm (o o) with body length 122–125 mm. Eyes open, apparently, at the age of about 30 days. Lactation lasts about 3 months and, on Pechora, proceeds mainly during the period of deep snow cover (Teplov, 1955). In a series of cases, tracks of a male were noted around a den with a litter, who, apparently, took part in the feeding of the young. On the Scandinavian Peninsula, no signs of male participation in the nourishment of young were observed (Krott, 1959). In the northern Urals, already in early July, the litter begins to lead a wandering way of life, and by the beginning of winter, they hardly differ from adults in size (Flerov, 1933).

In wolverines in captivity or tame animals in nature, from birth of the young to their attainment of sexual maturity, it is proposed to distinguish 5 phases (Krott, 1959).

The first phase is the first 4 weeks of life. Weight of males is 400-630 gm, of females—300-480 gm. In this time, they are still blind, bear the first juvenile pelage—a dirty-grayish-yellow tone. They drink their mother's milk exclusively.

The second phase is the 4th-10th week after birth. During this period, the weight of young wolverines reaches 3.3 kg. Lactation continues. The eyes open in the 5th week, and by the 8th week, males are 10% heavier than females. The first juvenile fur is replaced by the second—a dark-brownish color.

The third phase includes age of 10–24 weeks. At the age of 11 weeks, average male weight is 3.8 kg, of female, 3.5 kg. In this period, the second juvenile fur is replaced by the summer fur, but differs somewhat from that of adults and resembles the summer fur of pine martens. At the age of 20–24 weeks, the animals eat 400–500 gm of meat per day. Males begin to exhibit more activity than females.

The fourth phase includes the age of 6-12 months. At the beginning of August, the young wolverines don their winter fur. They begin to pursue live prey, but of dimensions no larger than themselves.

The fifth phase lasts from the age of 12 months to the attainment of sexual maturity. From the middle of April, the young

635

wolverines already have acquired their second summer fur, not differing from that of adults, and in mid-August of the second year of life, the winter fur of the adult animal. Summer marks the first cases of preying on hazelhens, but usually the wolverine's attention is not attracted by tetraonid birds. They make their first attempts to attack small livestock, without killing the victims. With the arrival of the second winter, a female tore apart a roe deer, and a young experimental male made an attempt to attack a small elk. In July, one in the 3rd year of life killed six sheep in one night.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. With the exception of man and wolves, the wolverine does not encounter any dangerous enemies within its basic range. For man, the wolverine is a difficult, occasional catch. In the Scandinavian peninsula, wolves destroy wolverines (Krott, 1959). Bear, lynx, red fox, Arctic fox and large eagles are dangerous for young in the den. When the young follow the mother, lynx and bear as well as wolves and man, are a danger to them. On being pursued by wolves, the wolverine jumps, if it is possible, into a tree. The damage caused by wolves must not be great, since in the taiga they [wolves] are rare, and the wolverine rarely transgresses onto the tundra (Krott, 1959).

All carnivorous animals, especially those ranging in size from red fox and lynx to bear may be, to a certain extent, considered as competitors of wolverines. But factually, carrion and remains devourers such as these which utilize the remains from the table of other carnivores are considered as food suppliers rather than competitors. In all events, with the presence of wolves in the region, however, their feeding regime is obviously improved and secondary and occasional food use decreases.

The diseases and parasites of wolverine have been poorly studied. In the upper Pechora, 21% of the wolverines caught were infected with nematodes. A significant number of the latter (47 to 243 individuals) greatly weaken the wolverine. In some cases, pathological changes of the internal organs and exhaustion are connected with physical defects (the loss of feet, etc.). Longevity is unknown.

Concerning fluctuations in numbers of wolverines, data are limited. In Pechora preserve, the number of tracks encountered over an 11-year period ranged from 0.02 to 0.04 along a 10 km route; *i.e.* two-fold. It was noted that the number of wolverines

increases parallel to the growth of the ungulate population in a given region.

Field characteristics. On the snow surface, the wolverine leaves well-defined prints of all its feet, with large well marked claws. In dimensions and its generally oval outline, it is reminiscent of the broad palm of an adult human.

The prints, which usually follow one another are almost always well distinguished because, even on the soft snow, the animal does not sink deeply. Walking in a straight line for a considerable distance is very typical for the wolverine. Excrement is rarely found along the track, usually not more than three times during a day's walk (P.Yu.).

Practical Significance

The practical significance of wolverine is contradictory. On one hand, it is a fur-bearing animal that provides a durable, warm and quite beautiful skin, though not expensive, and it sanitizes the taiga and tundra, destroying carrion and diseased and dying ungulates. On the other hand, with an increase in wolverine numbers, they begin to attack healthy animals, especially the young, and therefore in deer raising regions, they must be considered dangerous. In Sweden, the wolverine is considered a useful animal for the forest economy since it reduces in the number of ungulates in areas impossible for hunters to reach. The number of ungulates is, in many cases, very great and causes losses in the forest (Krott, 1959).

Wolverine systematically steals bait and lures from the traps of commercial hunters and steals stores from the hunter's cabins; therefore, they usually consider it an animal deserving of destruction the year round. In practice, this is difficult to realize. In the State preserves, if its numbers increase significantly, it must be limited.

The world catch of wolverine comprises about 6,000 skins. Its relative contribution in the USSR constitutes about 30%, and about 25% of the approximate number of animals in the USSR.

Wolverine is a very cautious animal, and different traps, in particular jawed traps, take them poorly. Setting the traps around carrion give somewhat better results. For hunting with dogs, ferocious and strong *laika* dogs are required, since the wolverine fiercely defends itself. Wolverine is very resistant to the action of poisons.

636

All methods for its capture are complicated by the vast area of its home range and its very long daily movement.

In the Scandinavian Peninsula, the best effect is attained by searching out litters, which is carried out in the second half of March and the first half of April. Two or three hunters on skis with a 2–3-week stock of food search a typical area for fresh tracks of a female leading to a den. In March, when the young are still blind, the female almost always occurs near the brood. She is first killed, and then the live young are taken. Abroad, the zoos pay 250 dollars for young wolverines 12–14 weeks of age.

In Sweden, the adult male hide is valued at 100 dollars, the female—70. Moreover, the hunters receive a bounty: 80 dollars for an adult wolverine and 40 for young. Deer breeder organizations also pay bounties for killed or captured wolverines (Krott, 1959) (P.Yu.).

Genus of Weasels and Polecats

Genus Mustela Linnaeus, 1758

- 1758. Mustela. Linnaeus. Syst. Nat., ed. X, 1, p. 45. Mustela erminea Linnaeus.
- 1775. Putorius. Frisch. Natur-System d. vierfüss. Thiere, p. 11.
- 1817. Putorius. Cuvier. Régne anim., 1, p. 147. Mustela putorius Linnaeus.
- 1829. Arctogale. Kaup. Entw. Gesch. Nat. Syst. Europ. Thierw. 1, p. 30. Mustela erminea Linnaeus.
- 1829. Ictis. Kaup. Ibidem. 1, p. 35, 40, 41. Mustela vulgaris Erxleben = Mustela nivalis Linnaeus.
- 1840. Foetorius. Keyserling et Blasius. Wirbelthiere Europas. p. 68. Mustela putorius Linnaeus.
- 1841. Gale. Wagner. Schreb. Säugeth. Suppl. 2, p. 234. Mustela vulgaris Erxleben = Mustela nivalis Linnaeus.
- 1841. Lutreola. Wagner. Ibidem. 2, p. 239. Viverra lutreola Linnaeus.
- 637 1871. Mustelina Bogdanov. Birds and animals of the chernozem belt of Povolozh'e (Tr. Obshch. estestvoisp. pri. Imp. Kazansk. Universit., 1, section 1, p. 167. Mustela erminea Linnaeus¹.

¹The mink was incorrectly referred to as the type of this genus by Ellerman and Morrison-Scott (1951), as well as the type of the following Bogdanov genus (which is correct).

- 1871. *Hydromustela*. Bogdanov. Ibidem, p. 167. *Mustela lutreola* Linnaeus.
- 1899. Eumustela. Acloque. Faune de France, Mamm., p. 62. Mustela vulgaris Erxleben (= Mustela nivalis Linnaeus) et Mustela erminea Linnaeus.
- 1911. Kolonokus. Satunin. Izv. Kavkazsk. muzeya, 5, p. 264. Mustela sibirica Pallas (V.H.).

General dimensions small or very small. The smallest species of the order belong to this genus.

The skull is usually relatively small, flattened in the majority, strongly elongated and narrow, without crests and protuberances. The braincase is voluminous and elongated, slightly widened in the occipital region, the facial part is short, weak and blunt, zygomatic arches are thin, weakly separated (often not as wide or just wider than the cranial part of the skull). Supraorbital processes are small, the interorbital and postorbital constrictions are weak or very weak or else the postorbital process is barely defined. The dorsal profile of the skull is usually straight and the convexity in the orbital region not developed or weakly developed; the profile of the facial portion is only slightly and gradually depressed. The diameter of the infraorbital foramena is greater than that of the alveolus of the upper canines; in some species, they are equal to it or even less.

In a few forms, the whole skull is wider and shorter, the braincase is relatively shortened and the facial part is strengthened, the zygomatic arches are relatively robust and more widely separated, the postorbital constriction is relatively well or even strongly defined, the convexity of the upper skull surface in the interorbital area is stronger, crests and protuberances, etc. are quite sharply developed. Some species have skulls of an intermediate character.

The auditory bullae in all species are notably swollen throughout the lower surface, usually of elongated bean-like form, and situated more or less parallel to each other; in some species, they are relatively shortened and the posterior portions are relatively more widely divergent than the anterior. The hook-like processes of the pterygoid bones are not united with the auditory bullae. The mammary (mastoid) processes are weakly developed, and the lateral occipital (paroccipital) are not developed. The bony palate is of moderate width. In general, with a comparatively large number of species, several of them have evident differences in skull structure, though in close species, they are not great (see later).

Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{3}{3} M \frac{1}{2} = 34$. There is no additional cusp

on the inner side of the main crest of the last lower premolar (third tooth behind canine—just anterior to carnassial). The lower carnassial tooth (first molar) has no additional cusp on the inner side of the median crest. The longitudinal axes of the crowns of the upper carnassial teeth lie at a significant angle to each other and with the longitudinal axis of the skull. The second upper premolar (first in the row) is very small, and correspond approximately in dimensions to the first [premolar] in martens (genus *Martes*), but it is not lost or this occurs only rarely.

The trunk is thin and strongly elongated, in some species to an extreme degree, and it appears as though "snake-like". The legs are short, in several, very short, the tail is of various lengths and may attain half or nearly half the body length. In several species it is short, and constitutes about 0.25 of the body length or less and perhaps equal the length of the hind foot. The head is relatively small, narrow, elongated and flattened, usually no broader in diameter than the neck, in some almost "snake-like" in appearance. The ears are small, very widely separated, rounded; the eyes are quite large. The extremities are digitigrade; palms and soles are moderately broad.

Anal scent glands are developed in all species, and in some very strongly; individuals are capable of spraying the secretion of these glands. All have a special "polecat" odor. Abdominal glands characteristic of wolverines and martens are absent.

The fur is dense, but usually not long, and in the majority, closely compacted; in some, quite fluffy, and more or less equal in length over the whole body. In the majority, the fur is soft and silky and in some, highly valued. In the majority, the tail is covered by short hairs and is relatively thin, but in some quite fluffy.

The color is quite variable—two-toned with a light venter, of monocolor ocherous or brown tones, or blackish-yellow with a dark venter. A distinct throat patch does not occur. In some species, there is a pattern on the head in the form of a "mask" of dark or, on the contrary, light color. In one species with monotone general color, there is a narrow white band along the whole back and on the belly (*M. strigidorsa*).

Seasonal dimorphism in density and length of the fur of northern forms is very pronounced, while in the south, it is weaker or even entirely unexpressed or nearly so. In some northern species, sharp seasonal dimorphism in color is very pronounced (whitening in winter), the sharpness of its manifestation in general and even the reality of change in color itself varies geographically within the limits of one species. Sexual differences in color and character of the fur are absent; in all species, females are smaller than males, in some quite significantly. There are 4 pairs of inguinal and abdominal mammae, or in several, 3.

All representatives of the genus are very energetic, quick, active and clever animals. The majority are able to climb trees, however, there are arboreal forms in the genus, and all of them are true terrestrial carnivores, usually moving in leaps, bending the back. All climb very well in windfalls, among rocks and in rodent burrows. They inhabit very diverse biotopes—from the Arctic and high mountains higher than 3000 m above sea level to steppes and deserts and tropical forests. All of them can swim—some species are typically amphibious forms associated with fresh water (minks). Some species do not avoid proximity to humans and even reveal some anthropophilous tendencies.

They are settled forms; monogamous; there are 1–2 and 3–4, to 10 young. Lairs are made in extremely varied places—among windfalls, in rocks, etc., but chiefly in underground burrows, mainly of rodents. They do not make nests in tree hollows, especially high above the ground. They are usually solitary animals, but several sometimes hunt in small groups (litters?). They are sharply distinctive carnivores, utilizing no plant food at all or almost none. The main prey are rodents of various sizes from mice and voles to large ground squirrels. The majority are miophagous*. Birds, reptiles and amphibians (frogs) are foods of secondary importance. Sometimes there is a quite close connection with particular species of rodents (the steppe polecat—ground squirrels, ermine—water vole, weasel—small voles etc.). Several forms are specialized for feeding on fish as well as amphibians, crawfishes etc. Hibernation or winter sleep does not occur.

The species of the genus are quite variable in size. The smallest (weasels) have, in several forms a body length from 130 mm (averaging about 160 mm) and a weight of less than 100 gm

^{*}Lit. "mouse-eaters". This seems to be a coined word-Sci. Ed.

(40-75 gm the smallest species of the carnivore order), and largest species (M. eversmanni)—[body length] to 565 mm.

The range of the genus is very vast and occupies the greater part of Eurasia and the northern part of North Africa, all of North America and a considerable part of South [America]. The northern limit of the range in America includes the whole mainland and the 640 entire Arctic archipelago and the northern and northeastern part of Greenland south to approximately 70° N. lat. or a little southward. The southern limit passes along the northern and northwestern part of South America. To the south it covers Venezuela and southwestern Columbia, to the west includes Peru and to the west and south the Bolivian Andes to the latitude of Lake Titicaca or a little southward, and passes to the Pacific Ocean. On the whole, on this continent, the representative of the genus (M. frenata) is mainly associated with montane regions where it attains a height of 3,000 m above sea level. Species of the genus are encountered on all of the islands of the Atlantic coast of North America and on all the islands of the Pacific coast, including Kodiak, but are absent in the West Indies. On the islands of the Bering Sea (Aleutians, Pribilofs, St. Matthew, Diomedes and others), it is absent except on Unimak¹.

In the Old World, the range occupies all of Europe except Iceland, the Arctic Islands and the islands of the Mediterranean Sea. In Africa, the range includes its extreme northwestern corner—Morocco, the parts of Algeria and Tunisia connected with the Atlas mountain system and Egypt, apparently, only Lower.

In Asia, the northern limit of the range occupies the entire mainland and the New Siberian Islands. The southern limit in Asia includes, to the south, Palestine, Syria and the northern half of Iraq. In Iran, the range occupies the northwestern part of the country, whence, it passes as a broad projection along the Zagros mountain system towards the southeast; however it does not extend far, not reaching the shores of the Persian Gulf (extreme southwest of the country is not included in the range). Farther on, the range occupies northern and northeastern Iran (representatives of the genus are absent over the entire central desert part), whence the border, apparently, to the south covers the Hindu Kush system, through

^{&#}x27;References of several authors (Carter, Hill and Tate, 1946) on the occurrence of weasel and mink on the Aleutian Islands, are apparently, mistaken and are not confirmed by other authors (Miller and Kellogg, 1955; Hall and Kelson, 1959). On Unimak, the existence of weasel and ermine was recorded (Murie, 1959).

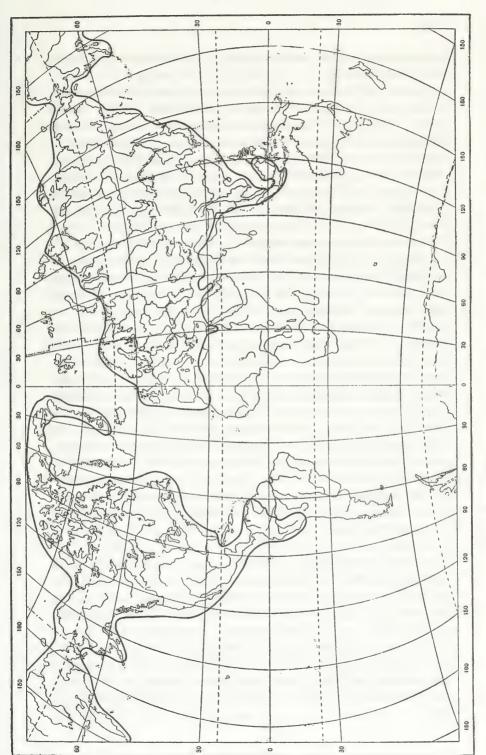


Fig. 233. Range of the weasel and polecat genus, Mustela L. V.G. Heptner.

Khazaradzhat (Hazara) and, apparently, the Kabul region and passes to India-to Chitral.

Farther to the east, the range occupies Kashmir and the entire Himalayas from Kashmir through Nepal, Sikkim, Bhutan, and to Assam inclusively. In southeast Asia, the range includes Burma. the Indochinese Peninsula, Tenasserim, Malacca and the islands of Sumatra, Java and Kalimantan (Borneo). Eastward the mainland range reaches the Pacific Ocean and includes the islands Karangin. Kuril (in part), Shantar, Sakhalin, the large Japanese [islands] (Hokkaido, Honshu, Shikoku, Kyushu) the Ryukyus, Taiwan and Hainan. On the Arctic Islands, except New Siberian, as in the Commander Islands, representatives of the genus are absent.

The range of the genus has not suffered noticeable changes on the negative side under the influence of human activity in the time under review. The ranges of some individual species have sometimes changed in recent times, either negatively or positively.

The scope accepted here of the genus (13 species) itself represents a quite heterogeneous group. The extreme members are a more or less natural series, which may comprise the species of the genus from the weasel, M. nivalis (races of the group rixosa) to the white polecat (M. eversmanni), differing from each other in many respects, among which are the craniological, significantly. On the other hand, in several characteristics, separate species within this series are obviously similar to each other. This gave an opportunity to various authors to divide the genus accepted here into separate genera or subgenera. Thus, separate groups were distinguished such as polecats (Putorius), true weasels and ermines (Arctogale), minks (Lutreola), Siberian weasels (Kolonokus) and Javan kolonok (Plesiogale) in part, combining in different ways the species in these groups.

At the same time, if we consider the group of species as a whole, it is sufficiently clear that strict delimitation of it into several is impossible, and the most extreme forms, as shown above, 641 are connected with each other by a series of intermediates. This applies all the more to other members of the genus. Therefore, it is natural to accept the large genus Mustela in which two subgenera only may be distinguished—the specialized polecats: subgenus Putorius and subgenus Mustela, to which belong all remaining species. Even separation into a subgenus of Siberian weasels and minks, which up to now has been accepted by some authors

(Stroganov, 1962) cannot be considered well founded if one considers all species of the genus. The polecats even now are sometimes separated into a separate genus (*Putorius*), that has been poorly received. The mink serves as a connecting link between them and the remaining species².

The identification of the actual systematic position of the genus among these various forms (genera) present in the subfamily, is very difficult. It is apparent, however, that this is a line of development in the subfamily different from the true martens and wolverine. It is more connected with the other genera of the subfamily (see above) than with Martes and Gulo ("Martinae" and "Guloninae" of some authors). Despite the presence in it of some specialized forms (subgenus *Putorius*), in its group of genera the genus Mustela must, apparently (in the pure systematic sense) be placed "in the foundation" of all groups of Mustelinae (except the two above-mentioned genera). This is indicated by the craniological structure of the species belonging to the subgenus Mustela (their specialization obviously proceeded in another direction, in particular the elaboration of a special form of the body). The genus Mustela, apparently, is more ancient—to it belong several forms from the upper Miocene of North America and Europe and from the lower Pliocene of Asia. The closeness of the connection between these fossil forms is not clear.

The following 13 species may be included in the genus (listed in order of increasing specialization): weasel, *M. nivalis* (including *M. rixosa* which American authors consider a separate species); ermine, or suslennik* *M. erminea*; solongoi, *M. altaica* Indian ermine; *M. kathiah* (sometimes this species is united with *M. altaica*); kolonok, Siberian weasel, *M. sibirica* (including the form *itatsi*, sometimes considered a separate species; Stroganov, 1962); long-tailed weasel, *M. frenata*; white-striped weasel, *M. strigidorsa*; naked-footed kolonok, *M. nudipes*; European mink, *M. lutreola*; American mink, *M. vison*; black or forest polecat, *M. putorius*; American polecat [black-footed ferret], *M. nigripes*; white

²An indication is that hybrids may exist between the black polecat and the Russian mink in nature. For details on relationships in the genus, and connections between the polecat group on one hand and a remaining species see section on polecats and mink.

^{*}Local name referring to suslik, or ground squirrel, which in many places is an important prey species—Sci. Ed.

or steppe polecat, M. eversmanni. The last three species belong to the subgenus Putorius, and the remainder—to subgenus Mustela.

Of the 13 species, two are Eurasian-North American (M. erminea, M. nivalis, the latter also in North Africa), 1 is North and South American (M. frenata), 2 are North American (M. vison, M. nigripes), 2 are European (M. putorius, M. lutreola, the latter also in the Caucasus), 3 are South Asian (M. kathiah, M. strigidorsa, M. nudipes), and 3 are Central Asian and Siberian (M. eversmanni, M. sibirica—penetrating also into eastern Europe; M. altaica).

They are fur-bearing species, and are destroyers of rodents and regulators of their number.

The indigenous fauna of the USSR comprises 7 species: 1) weasel, M. (M.) nivalis Linnaeus, 1758; 2) ermine, M. (M.) erminea Linnaeus, 1758; 3) solongoi M. (M.) altaica Pallas, 1811; 4) Siberian weasel [kolonok], M. (M.) sibirica Pallas, 1773; 5) Russian mink, M. (M.) lutreola Linnaeus, 1761; 6) black or forest polecat, M. (P.) putorius Linnaeus, 1758; 7) white or steppe polecat, M. (P.) eversmanni Lesson, 1827. One species—the American mink, M. (M.) vison Schreber, 1777—has been acclimatized.

Species of the genus occupy the entire territory of the country and are encountered in all biotopes. They play an important role in fur trade, and in part as regulators of populations of rodents—pests of agriculture and transmitters and reservoirs of dangerous diseases of humans and domestic animals (V.H.).

642 Key for Identification of the Species in the Genus Mustela

- 1 (4). Color of entire body monotone white (winter) or lower side of body pure white (sometimes with light grayish-yellow highlights), upper side various brownish or sandy tones (summer). Color of upper lip and chin not differentiated from that of surrounding parts of head. Color borders on sides well marked. Skull moderately elongated—distance between mastoid (mammary) processes approximately equal to half of condylobasal length of the skull.
- 2(3). Distal half or third of tail pure black. Tail length with terminal hairs equal to half of body length or somewhat more. Width of skull below canines notably less than width of interorbital area. Condylobasal length of male

- skull is up to 53 mm, of female—up to 46 mm ermine, M. (M.) erminea (page 995).
- 3(2). Tail monotone along entire length (there may be individual dark hairs at its extreme end). Length of tail with terminal hairs significantly less than half, usually less than one-third, of body length. Width of skull below the canines approximately equal to width of interorbital area. Condylobasal length of male skull up to 47.2 mm; of female up to 36.7 mm weasel, *M.* (*M.*) nivalis (page 965).
- 4(1). Color otherwise. If dorsum tawny and brown tones, and venter light and border between dorsum and venter colors on sides well marked, then distal half of tail not black and not sharply differentiated from color of basal portion and length of tail with terminal hairs about half to more one-third of body length³. Skull moderately or greatly elongated or relatively short and broad.
- 5(8). Lower surface of body, except throat and chin and sometimes middle of abdomen, black or blackish, darker than dorsal side; legs always black. Entire tail or its distal half black. Skull short and broad—distance between the mastoid processes considerably greater than half of condylobasal length of skull.
- 6(7). Dorsal body color dark with black color predominant, through which very light yellowish underfur shines through, especially on sides; venter black or blackish. All or almost all of tail (except very base) black. Black color of legs not sharply contrasting with color of trunk. Postorbital part of braincase has no well-defined isthmus and its edges form parallel or almost parallel lines black polecat, M. (P.) putorius (page 1107).
- 7(6). Color of upper body light with yellow color predominant, because light underfur is weakly covered by dark-brown guard hairs; venter light, yellowish. Only distal half of tail black; basal part has light color of back. Black leg color sharply contrasting with color of trunk. Postorbital part of braincase with well-defined isthmus, and its edges form angled lines, corners directed towards each other steppe (white) polecat, *M.* (*P.*) eversmanni (page 1133).

 $^{^3}$ An exception is present in some races of solongoi [M. altaica]; see 14 (13) and text.

643

- 8(5). Color of abdomen and lower side of body not black or blackish, legs not black, tail without black color, its color corresponds to upper body. Skull moderately elongated or extended (mastoid width of skull constitutes about half, or less than half, condylobasal length of skull).
- 9 (12). Color of entire body monotone—dark tawny-brown with dark undercoat; venter not lighter than dorsum. Small white marks only on lips and chin, sometimes on chest. Skull moderately elongated—distance between mastoid processes constitutes about half of condylobasal length of skull.
- 11 (10). Only lower lip white. Least width of skull behind supraorbital processes less than interorbital width. Upper molar relatively large and longitudinal diameter of its inner blade markedly greater than diameter of outer. Posterior end of second premolar contacts carnassial tooth somewhat more mediad to antero-outer corner of carnassial tooth American mink, M. (M.) vison (page 1391).
- 12 (9). Entire body color if not monotone is not dark tawnybrown, but bright yellowish red or dull yellowish-strawsandy, or below is somewhat lighter than above, or vice versa. Skull elongated—distance between mastoid processes is usually less than half of condylobasal length of skull.

14 (13). Dark "mask" on muzzle absent. Postorbital constriction of skull short, its lateral outlines not parallel and forms a sharp isthmus directly behind supraorbital processes. Color is bright or dull, yellowish-red, lower side a little to considerably lighter than upper, perhaps almost dirty-white with ocherous highlights, boundary between colors of dorsum and venter sharp or transition between them gradual. Dimensions smaller (condylobasal length of skull of males less than 55 mm, of females—less than 48 mm)solongoi M. (M.) altaica (page 1030) (V.H.).

Subgenus of Weasels

Subgenus Mustela Linnaeus, 1758

WEASEL1

Mustela (Mustela) nivalis Linnaeus, 1766

- 1766. *Mustela nivalis* Linnaeus. Syst. Nat., ed. XII, 1, p. 69. Westerbotten province, Sweden².
- 644 1777. Mustela vulgaris Erxleben. Syst. Regni Anim., 1, p. 471. Umerennaya Evropa [Temperate Europe]. After Ognev (1935)—Vic. Leipzig.
 - 1800. *Mustela boccamela*. Bechstein. Pennant. Übers vierf. Thiere, 2, p. 395. Sardinia.
 - 1811. Mustela gale. Pallas. Zoogr. Rosso-Asiat. 3, p. 94. Renaming of vulgaris.
 - 1877. Mustela stoliczkana. Blanford. J. Asiat. Soc. Bengal, 46, 2, p. 260. Yarkand.
 - 1896. Mustela rixosa Bangs. Proc. Biol. Soc. Washington, 10, p. 21. Saskachewan, Canada.
 - 1899. *Mustela nikolskii*. Semenov. Zap. Akad. nauk, ser. 8, vol. 6, p. 14. Vic. Simferopol, Crimea³.
- ¹The correct spelled name for this species is undoubtedly, *lazka*, and is derived from the verb *lazat*' [=to climb]. The ability of the animal to climb with extraordinary agility, especially among fallen limbs etc., is striking, and immediately calls attention to itself.

²Westerbotten province lies between 60° and 61° N. lat. and therefore, often encountered references to the type locality, said to be in northern Sweden, are incorrect. This has substantive nomenclature significance.

³This form is incorrectly cited in Ellerman and Morrison-Scott (1951).

- 1900. Putorius nivalis pallidus. Barrett-Hamilton. Ann. Mag. Nat. Hist. 5, p. 48. Kokand, Fergana.
- 1900. Putorius nivalis caucasicus. Barrett-Hamilton. Ibidem, p. 48. Caucasus, Gochal (?) mountains, 12000'.
- 1901. Mustela (Ictis) dombrowskii. Matschie. Sitzungsber. Ges. naturf.-Freunde Berlin, p. 231. Siul'nita. Romania.
- 1903. Putorius (Arctogale) pygmaeus. J. Allen. Bull. Amer. Mus. Nat. Hist., 19, p. 176. Gizhiga, northern shore of Okhotsk Sea.
- 1907. Putorius nivalis dinniki. Satunin. Izv. Kavkazsk. muzeya, 3, p. 105. Stavropol (Caucaskii).
- 1911. *Ictis boccamela nikolskii*. Satunin. Izv. Kavkazskovo muzeya, 5, p. 257. Crimea⁴.
- 1921. Mustela rixosa namiyei. Kuroda. Journ. Mamm., 2, p. 209, Aomori, northern part of Honshu (Hondo) island, Japan.
- 1922. Ictis nivalis var. kamtschatica. Dybowski. Arch. Tov. Nauk. Lwow, 1, p. 349. Nomen nudum.
- 1926. Mustela punctata. Domaniewski. Ann. Mus. Zool. Polonici. N.H. 5, p. 55. Darasun; southern Trans-Baikaliya.
- 1927. Mustela nivalis mosanensis Mori. J. Chosen. N.H. Soc., 5, p. 28. Iengan near Mosan, Korean Peninsula.
- 1936. Mustela pygmaea yesoidsuna. Kishida. Dobuts Zasshi, 48, 4, p. 177. Hokkaido, Japan.
- 1936. Mustela pygmaea karaftensis. Kishida. Ibidem, p. 177. Sakhalin.
- 1937. Mustela trettaui. Kleinschmidt. Falco, 33, p. 11. "Germany".
- 1952. Mustela nivalis kerulenica. Bannikov. Byull. Mosk. Obsch. Isp. Prirody, 57, No. 2, p. 40. Vic. Undurkhan on Kerulen [r.], Mongolian Republic.
- 1953. Mustela nivalis heptneri. Morosova-Turova. Zool. Zhurn., 37, No. 6, p. 1267. Egri-Gek—tributary of Kushka [river], Badkhyz; southern Turkmeniya (V.H.).

Diagnosis

Coloration monotone white, or dorsum dark tawny tones, and venter white, with color boundary between dorsum and venter sharply demarcated. Distal half of tail not black. Tail length

⁴Satunin, apparently, not knowing of the work of Semenov, describes the Crimean weasel as a new form.

significantly less than half of body length, usually not more than one third. Skull is moderately elongated—distance between mastoid (mammary) processes approximately equal to half of condylobasal length of skull. Width of skull below canines approximately equal to interorbital width. Dimensions small to very small (V.H.).

Description⁵

The general appearance of the weasel is very characteristic. It has a thin, greatly elongated, extremely flexible body with a small, somewhat elongated head with a small, blunt muzzle. The head is narrow, not thicker than the neck; the eyes are quite large, dark and slightly bulging; the ears are situated wide apart, short and rounded. The legs are short, the feet of moderate breadth. The tail is relatively short. It is considerably less than half the body length, as a rule not greater than one-third of its length, sometimes not as long or slightly longer than the hind foot, and in individual cases, even shorter than the hind foot, covered with short, close-lying hairs, and appears thin, not fluffy. The lower surface of the front and hind are feet covered with hairs, the claws are not long, but very sharp, dark.

The small head, long neck and thin, elongated body (where the head can go, so can the body) confers on the weasel, especially with its extreme mobility, a unique "serpentine" appearance. When moving, the weasel proceeds by jumping, strongly bending the back; "creeping" very quickly and nimbly among rocks, brushwood, rodent burrows etc.

Winter fur is dense, but short, and quite closely-fitting; in northern forms, it is soft and silky and in southerly forms, coarser. In summer it is very short, sparser and rougher. In northern form of the species, variations in characteristics of winter and summer fur are considerable, but in southern forms, much less. Summer, coloration is bi-colored—the lower body including the lower jaw and inner sides of the legs are white. Sometimes the palms and the lower parts of the anterior extremities and the toes of the posterior are partially or completely white. The upper is dark and in different races, varies greatly—from dark-tawny or dark-chocolate to light pale tawny or sandy. The color of the dorsum extends to the

645

⁵In the case of characteristics of this species, some unpublished materials, made available by L.G. Morozova-Turova, were used.



Fig. 234. Weasel, Mustela (Mustela) nivalis L. Sketch by A.N. Komarov.

outer side of the legs; the tail has the same color as the back. The boundary between colors of the dorsum and venter on the sides is straight but sometimes forms an irregular line. There are sometimes dark-tawny spots on the white lower surface of the body, more often behind the corner of the mouth.

The color in winter is pure white and only in the form of rare exceptions do individual dark (black) hairs occur on the very end of the tail, but a black tail tip is not formed. Only the most southerly forms do not whiten at all in winter, or only some lightening in color may take place, or the side becomes white, but the white color does not cover the middle of the back. When molting, the animals sometimes become piebald—irregular dark parts are scattered over a white field.

Individual differences in fur color are in general insignificant, however, in various races, the amplitude of these differences is different and in several (Western Europe), these differences may be quite great. In particular, there is variation in the character of the boundary of coloration between the dorsum and venter and the frequency of appearance of dark marks on the light field, especially the lower jaw. Age and sex differences in color are absent, but geographic is, as shown, significant.

645

The skull is moderately elongated, with a voluminous, quite broad and swollen brain case. Its anterior region (in the area of the frontal bones) is wide and voluminous, the postorbital constriction is well-defined, but short and not deep. Facial parts of the skull are weak and very short. Width of the skull above the canines is approximately equal to interorbital width. The zygomatic arches are moderately divergent (zygomatic width approximately corresponds to greatest width of the skull posteriorly), thin and weak. The infraorbital foramen is small; its transverse diameter is approximately equal to the longitudinal diameter of the canine alveolus.

The upper profile of the cranial region of the skull is slightly flattened and the interorbital area does not form a significant elevation on it. Sculpturing of the skull is weak—the arrow-shaped [sagittal] crest is not defined or weakly defined in the posterior part, the occipital is relatively more strongly developed, but is not considerable. The auditory capsules are bean-like in form, convex and their inner edges are parallel. The distance between them is approximately equal to the width of the hard palate at the level of the anterior border of the sphenopalatine notch. Teeth are relatively small, but the carnassial tooth is developed and the canines are long and strong, although thin.

On the whole, the weasel skull, especially that of the smallest forms (rixosa group) has infantile features as compared with other closely related species of the genus (ermine, Siberian weasel). These are expressed in the relatively large size of the entire cranial portion, in the size of its anterior part (on the extension of the zygomatic arches—the frontal part), in the unusual shortening of the facial part, the weak development of the crests and in general sculpturing. Apparently, here, as well as other likely reasons, the phenomenon of allometry may also be expressed.

Individual variation in the skull is considerable in all characters. The sexual is illustrated by the fact that the skull of males is larger, and wider in the mastoid part, the postorbital constriction is absolutely and relatively narrower, and crests, tubercules etc. of the skull are more strongly developed.

Age variation of the skull is insignificant. In young animals, the brain case is still of relatively greater size than in the adults and is more swollen. It is characteristic that the sequence of age changes in the skull is small and take place so quickly that the skull of a young weasel in the first winter is only a little different

from that of the adult. The complete fusion of the skull sutures occurs relatively very early—earlier than in the large members of the genus.

Geographic variation of the skull, in accordance with the generally large variation of the species, is very great. It is expressed both in general dimensions and also in general structure and proportions of its parts. In the small forms, infantile features are more strongly developed than in large forms. In the latter, in connection with the strengthening of protuberances, crests and other features, similarity to the ermine skull in particular increases. The degree of sexual dimorphism in dimensions changes geographically—in the smallest forms, it is almost unexpressed, but grows with the increase in general dimensions and is well developed in the largest races.

The os penis is sharply bent upwards at its distal end, and here is formed a hook, characteristic of the majority of species of this genus.

The dimensions of weasel are subjected in some races to great individual variation, rarely found among mammals in general. Thus, in the race vulgaris, the weight of the largest individuals may exceed the weight of the smallest by almost four times (35 and 130 gm). In some large races males may be almost 1.5 times larger than females (body length). Geographic variation in dimensions is 648 very great, greater than that in other species of the family. The average weight of animals of large races may be 2-3 times more than that of small races. Weight of individual animals of the large forms may exceed the average weight of small races by 7-8 times. Not only absolute dimensions and weight vary geographically, but also the amplitude of their individual variation. Geographic variation in relative tail length is characteristic—in various races it constitutes from 13 to 30% of the body length. In the extreme case, in individual animals the tail length may be less than that of the hind foot length or equal to it.

Body length of males is 130-260 mm, of females, 114-204 mm; tail length of males is 12-87 mm, of females, 17-60 mm; length of hind foot of males is 16-42 mm, of females, 17-33 mm; height of ear of males is 10-16 mm, of females, 8.8-12.8 mm.

Condylobasal length of the male skull is 22.8–47.2 mm, of females, 27.5–36.7 mm; mastoid width of males is 11.0–22.4 mm, of females, 12.5–18.9 mm; interorbital width of males is 5.0–10.8

mm, of females, 5.5–7.8 mm; postorbital width of males is 6.8–9.0 mm, of females, 6.2–8.0 mm; zygomatic width of males is 13.8–26.0 mm, of females, 13.8–19.2 mm. Length of the os penis is 12–20 mm.

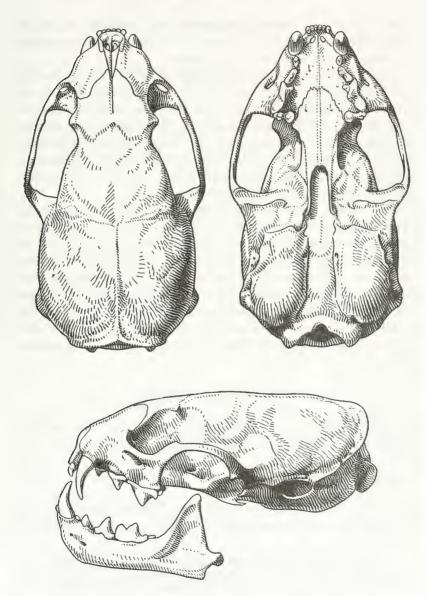


Fig. 235. Skull of weasel, Mustela (Mustela) nivalis L.

Weight of males is 36-250 gm, of females, 29.5-117 gm⁶ (V.H.).

Systematic Position

Weasel is itself an entirely specialized form; however, within the limits of the genus *Mustela*, it is, apparently, properly placed at the beginning of the entire series of species.

In several respects, it is, compared to all remaining species, less specialized. This is shown, first of all, by the above-mentioned "infantile" features of its skull. As mentioned before, these infantile features are associated, to a considerable degree, with the very small dimensions of the animal, and are particularly distinct in the small forms (rixosa group), but they are strong even in its large races, which give up little in dimensions to the ermine (weasels of the boccamela-heptneri group).

The weasel stands nearest of all to the ermine (M. erminea), although they differ in a series of essential characteristics, including the structure of the os penis. It is probable that this is one of the details of the mechanism of reproductive isolation where both species are morphologically closer to each other in areas simultaneously inhabited by them (Tien Shan). The weasel is connected through the ermine with M. altaica with which it does not differ in structure of the genital organs. On the whole, it is quite a close group, noteably distanced from the larger species of the genus (V.H.).

Geographic Distribution

The temperate, and in part, the arctic zone of the New and Old Worlds; in the Old World, also in part the subtropical zone.

Geographic Range in the Soviet Union

This occupies essentially the entire State territory and constitutes the greater part of the range of the species in the Old World.

⁶Dimensions of body and skull after Stroganov (1962) and unpublished material of L.G. Morozova-Turova; os penis dimensions after Ognev (1935); weight and other data also from the collections of the Z[oological] M[useum of] M[oscow] U[niversity]. Minimum dimensions of females are exaggerated.

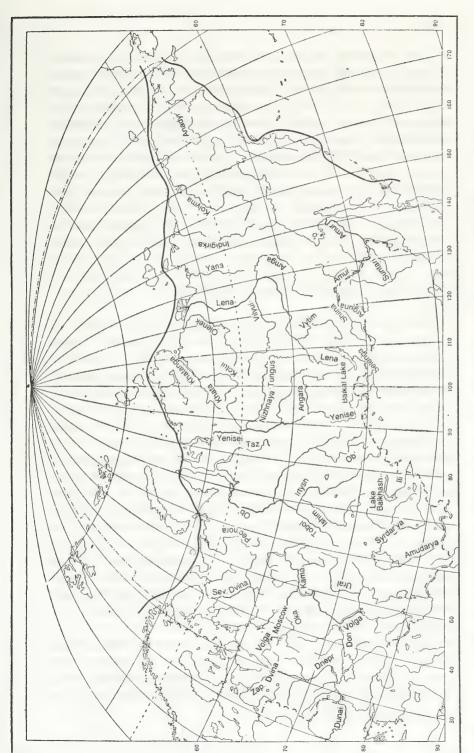


Fig. 236. Boundary of the distribution of the weasel, Mustela (Mustela) nivalis L. in the USSR. V.G. Heptner.

In the north, the range extends to the shore of the Arctic Ocean. The weasel is absent on the islands of the Arctic Ocean, except Bol'shoi Lyakhorsk. Occurrence of weasel on Karaginsk Island was not recorded; it is absent on the Commanders; it is, apparently, found on Shantar Islands, although there is no positive information about it. It inhabits Sakhalin (information on the absence of weasel here is mistaken); of the Kuril islands, it is present only on Kunashir; the possibility that it may be met with in some of the southern islands is not excluded. In spite of some assertions, it is also found in the Kyzylkum and Karakum. It is not excluded that the weasel does not reach the extreme north of Taimyr, and information about its occurrence in the Pamir are not completely definite.

650 Geographic Range outside the Soviet Union

Includes all Europe, including England (absent in Ireland), the islands of the Mediterranean Sea (Balearic, Sardinia, Corsica, Sicily, Malta and Crete; apparently absent in Cyprus), Algeria and Morocco (and probably Tunisia), the Azores (the weasel probably was introduced into Malta and the Azores), and Egypt (Lower).

In Asia, it is encountered in Asia Minor and northern Iraq. In Iran, it occupies the northern, northwestern and northeastern parts of the country; from the northwest, the range extends quite far to the southeast as a projection along the Zagros mountain system. It exists in northern Afghanistan, Kashgaria (known to the east as far as Lobnor), in Dzhungaria, in the northern part of the Mongolian Republic including to the south the Mongolian, and, probably, Gobi Altai and Trans-Altai Gobi, Khangai and the Kerulen [river]* region, in northeastern China (former Manchuria), on the Korean Peninsula and in Japan. In China, it is apparently absent in Inner Mongolia and Tibet. The extent of its distribution to the south in the eastern parts of China is unknown. It scarcely goes far south, although one of the forms was recorded in Tonkin (North Vietnam) however as doubtful.

In the New World, the weasel is distributed in the northern half of North America to the northern shore of the mainland. Just west of Hudson Bay the northern border passes [westward] along a line from Chesterfield [Inlet] on the [west] coast of the Bay to

^{*}Now called Cherlen Gol-Sci. Ed.

Bathurst Inlet on the northern shore, south of Victoria Island. The southern border is itself represented by a complicated line passing from the coast of the Pacific Ocean at Juneau through British Columbia, the southwestern corner of Alberta and northern Montana. The range includes North Dakota, a great part (except western) of South Dakota and Nebraska, Iowa, the northern part of Illinois and Indiana, Ohio, and almost all of Pennsylvania and West Virginia. From here, a small extension of the range directs itself to the southwest, reaching the northwestern corner of South Carolina.

Farther east, the border passes at first along the Saint Lawrence river, and then crosses the eastern extremity of Lake Huron, going along its eastern shore, then along the southern shore of Lake Erie and thence turns towards the southeast, crosses Pennsylvania and reaches the Atlantic Ocean. It is absent in Newfoundland (V.H.).

Geographic Variation

Geographic variation in the weasel is not only very great, but also complicated and itself is considered one of the most interesting cases of geographic variation among mammals. The systematics of the weasel then and now led and lead to fundamental disagreements.

Even at the beginning of the past century, it was noted that in Europe, among large, comparatively long-tailed weasels, there were encountered very small short-tailed ones. Later this form received the name *M. minuta*, and began to be considered as a category of distinct species, existing in several parts of Europe among populations of the larger common weasel—*M. nivalis* (*M. vulgaris*). Later, it was established that in Siberia as well as in the Far East, in Japan and in northern Europe, only the small short-tailed weasel exists. Already in the current century, it was proposed that these forms be attributed to the American "species", *M. rixosa* (Kuroda, 1921). Later (G. Allen, 1933), the Central and West European small weasels which were given the name *M. minuta* were related to the species *rixosa*. In this way, representations concerning the two species of weasels in the Palearctic were affirmed and each of them had its own geographical races (subspecies).

Everything was complicated by the fact that, along the southern border of the species range of the large weasel (Mediterranean), the

existence of a particularly large forms was recorded, which some authors were inclined to consider a separate species (M. boccamela). This opinion, on the contrary, had been rejected much earlier, but the representation of species independence of the European M. minuta was still held by some western authors in the 40's and even the end of the 50's (Van den Brink, 1958). American authors, up- till now, consider their weasel an independent species—M. rixosa and that the small weasels of Asia and Europe belong to its subspecies.

In actuality, a long time ago it was accepted by our systematists (Ognev, 1935, for example), that in the whole Palearctic only one weasel species exists, geographically very variable, with a complicated internal structure. Its extreme forms (pygmaea-heptneri) are so strongly differentiated that with limited material (territorial or quantitative) and insufficiently worked out theoretical prerequisites, they are actually very easily accepted as different species. Other European investigators gradually came to agree with the concept of species unity (Ellerman and Morrison-Scott, 1951; Zimmermann, 1959 and others). It is also doubtless that the weasels of North America are nothing more than a subspecies or group of subspecies of M. nivalis. Their specific identity with the small weasels of Asia was shown long ago (G. Allen, 1933).

Details of geographic variation, relationships between the various races, their origin and formation, etc. still demand further clarification with large samples. At the present time, the following scheme of geographic variation in weasels may be provisionally accepted for our fauna.¹¹

All subspecies of weasel may be divided into 3 groups well-characterized morphologically and regularly localized geographically: 1) small weasels of the group *pygmaea-rixosa*; 2) large weasels of the group *boccamela* and 3) races of intermediate type of the group *nivalis*.

A. Subspecies of the group pygmaea-rixosa, small weasels.

Very small weasels with very short tails and small skull of the infantile type; in our country, they become completely white in winter.

¹¹In the description of infraspecific geographic variation of weasels, the unpublished material, kindly made available by L.G. Morozova-Turova, was used equally with other materials.

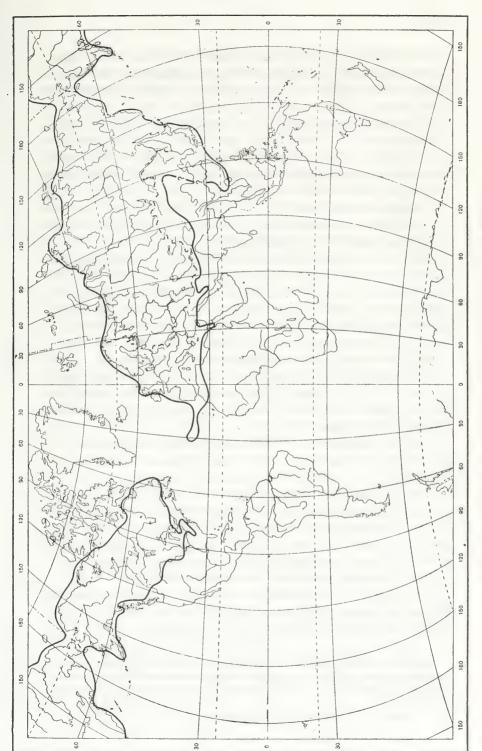


Fig. 237. Species range of the weasel, Mustela (Mustela) nivalis L. V.G. Heptner.

Northern European part of the country, Siberia, and Far East. Outside the USSR—Finland, northern Scandinavian Peninsula, Mongolian Republic, northeastern China (former Manchuria), Japan, North America.

Weasels of this group are the smallest of all forms of the Carnivora.

1. Siberian weasel, M. (M.) n. pygmaea J. Allen, 1903 (syn. kamtschatica, karaftensis; with respect to the weasel of the Kuril Islands, the name namiyei was applied).

Dimensions very small.

Tail short, its length equal to hind foot or a bit longer and constitutes about 13% of body length.

In summer coat, dorsal color dark-brown, very rarely lighter, reddish. In winter, entirely white. Hair length on sacrum, 10.3 mm in summer and in winter 14 mm. Skull small, with weakly developed postorbital processes, short and wide postorbital constriction with weakly developed crests even in fully adult individuals.

Body length of males (32), 133-M160-172 mm; tail length, 12-M22.6-28 mm; hind foot length, 16-M21-25 mm.

Condylobasal length of male skull, 22.8-M32.7-34.8 mm; mastoid width, 11.0-M15.2-16.8 mm; interorbital width, 5.0-M7.2-8.2 mm; postorbital width, 7.0-M8.0-8.5 mm; zygomatic width, 13.8-M16.5-19.8 mm.

Weight of males (14), 37-M52.6-68 gm, of females (6), 29.5-M41.0-62 gm (material in Zoological Museum of Moscow University)¹².

All of Siberia, except southern and southeastern Trans-Baikaliya; northern and middle Urals, in northern Kazakhstan (a few south of Syr-Dar'ya mouth), and Far East including Sakhalin and Kuril Islands, northern European part of the USSR westwards to Kola Peninsula and southwards to northern parts of Kirovsk and Gor'kovsk districts. A few as far as Moscow district.

Outside the USSR—Finland, northern part of Scandinavian and Korean peninsulas, Mongolian Republic except eastern part and probably northeastern China (former Manchuria).

¹²Data of males and females combined (21)*: 29.5-M49.3-68 gm. Material from Sakhalin and Kamchatka to Altai. Animals from Perm district, belonging to this form or approaching *nivalis* average, apparently, somewhat larger: males (5) 50-M60.8-70 gm.

^{*} Apparently includes one unsexed animal-Sci. Ed.

In the European part of the Union, the most typical weasels are in the most northern parts of the range. In the more southern parts of the described region, weasels are locally mixed with forms of group *nivalis* or transitional populations.

It is possible that, in actuality in the vast territory outlined, the population is not systematically homogenous and there may be distinguished forms here differing from true pygmaea. Thus, it is possible that weasels of the southern part of the Far East themselves represent a distinct form (it apparently can be given the name mosanensis or namiyei); the position of Sakhalin and Kuril weasels is not clear, etc.; West Siberian weasels (except northern) are sometimes assigned to nivalis (Stroganov, 1962), etc.

2. Trans-Baikal weasel, M. (M.) n. punctata Domaniewski, 1926 (syn. kerulenica).

According to dimensions and relative tail length (tail constitutes about 13.9% of body length), it corresponds with M. (M.) n. pygmaea, but according to color of summer fur of upper body, is somewhat lighter. In winter, it becomes completely or almost completely white. Skull somewhat wider in its rostral portion, postorbital constriction somewhat sharper, and sexual dimorphism more weakly displayed than in M. (M.) n. pygmaea.

Body length of males (8), 150-M166.6-185 mm, tail length (11),* M20.2-28 mm; length of hind foot, 12-M18.2-23 mm¹³.

Condylobasal length of male skull (6), 31.0–M32.4–35.0 mm, of females (8), 27.5–M30.4–32.0 mm; mastoid width of males, 12.5–M14.3–16.0 mm; interorbital width of males, 6.6–M7.2–8.5 mm, of females, 5.5–M6.3–7.5 mm; postorbital width of males, 6.5–M7.4–8.0 mm, of females, 6.2–M6.9–8.0 mm.

Weight of males (9), 36–M48.6–84 gm, of females (7), 41–M48.7–63 gm. 14

Southern and southeastern Trans-Baikaliya.

Outside the USSR—eastern part of Mongolian Republic, and probably northeastern China (former Manchuria).

¹³Dimensions of animals from eastern part of Mongolian Republic. Materials in Zoological Museum of Moscow University.

¹⁴Weight of 21 specimens from collection of Z[oological] M[useum of] M[oscow] U[niversity] including individuals, the sex of which is not shown: 30–M46.8–84 gm. Weight of female with 11 large embryos, 94 gm. Data on weight on material from eastern part of Mongolian Republic (Choibalsan on Kerulen). Materials of Z[oological] M[useum of] M[oscow] U[niversity].

*Minimum value omitted in Russian original—Sci. Ed.

This form has its main area of distribution outside the boundaries of the USSR and reaches us only on the edge of its range. Lightening of body color is, apparently, connected with occupation of more arid regions.

B. Subspecies of the group boccamela, large weasels.

Weasels of very large dimensions, with large skull and relatively long tail and lighter, sometimes very light color; locally, they do not turn white, or not completely white, in winter. Infantile features, characteristic of weasels of the preceding group, are not developed, or only weakly. Skull relatively rough, with better developed crests, sexual dimorphism is sharply marked.

Trans-Caucasus, from western Kazakhstan to Semirech'e, and in the flat deserts of Middle Asia.

Outside the USSR—southern Europe (Mediterranean), Asia Minor, Iran, Afghanistan.

3. Trans-Caucasus weasel, M. (M.) n. boccamela Bechstein, 1800. Dimensions very large, tail very long, considerably longer than hind foot, constituting about 30% of body length.

In summer fur, color of upper body light brownish or chestnut, with yellowish or reddish tints. In some individuals, a brownish dot behind the corner of the mouth and sometimes on chest and belly. Winter fur not so pure white as in more northern forms; some animals in winter are piebald in color—dirty white with brown patches, some do not turn white at all.

Skull very large with marked constriction behind infraorbital processes.

Body length of males (20) 209–M226.5–260 mm; tail length, 55–M72.3–85 mm; length of hind foot, 22–M39.5–42 mm.

Condylobasal length of male skull, 41.0–M42.1–46.2 mm; of females (6), 29.8–M31.2–36.0 mm; mastoid width of males, 20.0–M20.2–22.4 mm; of females, 14.0–M15.1–16.8 mm; interorbital width of males, 8.5–M9.5–10.0 mm; of females, 6.2–M7.1–7.5 mm; postorbital width of males, 6.8–M8.8–8.4 mm; of females, 6.0–M7.1–8.0 mm; zygomatic width of males, 21.5–M22.6–24.0 mm. Weight of two males, 160 and 181 gm.

Trans-Caucasus.

Outside the USSR—southern Europe, Asia Minor, and probably western parts of Iran.

The weasel of Trans-Caucasus does not have any essential differences from the South European. However, among the latter,

apparently individuals may often be found possessing brownish dots on the chest and belly.

4. Middle Asiatic, or Turkmenian weasel, M. (M.) n. heptneri L. Turova, 1953.

Dimensions very large, in general corresponding with preceding form. Tail very long, considerably longer than hind foot and constitutes 25–30% of body length.

In summer fur, color of upper part of body very light, "desertish"—brownish-sandy or pale-yellowish, lighter than in all other forms of the species inhabiting our country. Fur short, sparse and coarse, in winter does not turn fully white. Length of hairs on the sacrum 5 mm in summer and 7 mm in winter.

Skull large and massive with widely separated zygomatic arches. Body length of males (7), 230–M234.1–242 mm; tail length, 55–M68.2–87 mm; length of hind foot, 27–M33.2–35 mm.

Condylobasal length of male skull, 40.5–M43.1–45.5 mm; mastoid width, 21.0–M21.3–22.0 mm; interorbital width, 9.8–M10.3–10.8 mm; postorbital width, 7.8–M8.3–9.0 mm; zygomatic width, 23.4–M24.4–26.0 mm.

Weight up to 250 gm (male from southern Tadzhikistan; Z[oological] M[useum of] M[oscow] U[niversity].

Level semideserts and deserts of southern Kazakhstan and Middle Asia from Caspian Sea to Semirech'e and southern Tadzhikistan, Kopet–Dag.

Outside the USSR—in Afghanistan and the northeastern part of Iran.

C*. Subspecies of the group nivalis, average weasels.

Weasels of moderate general dimensions, with tail of moderate length, very diverse in all characteristics of skull and body measurements. Sexual dimorphism well developed.

Middle and southern regions of the European part of the country; Crimea, Cis-Caucasus and northern Caucasus, western Kazakhstan, southern, and in part, middle Urals, montane parts of Middle Asia except Kopet-Dag.

In all respects—as well as in distribution—subspecies of this group occupy an intermediate position between the small group (group A) and the large group (group B) of subspecies.

5. Middle Russian weasel, M. (M.) n. nivalis Linnaeus, 1758 (syn. gale).

^{*}Misprinted B in Russian original-Sci. Ed.

Dimensions moderate, tail of moderate length—about 20-21% of body length and about 1.5 times greater than length of hind foot.

Color of upper body in summer fur is dark-brownish or chestnut, rarely lighter—yellowish-brownish. Winter fur pure white. The hair length on sacrum 9.5 mm in summer, and in winter, 12.5 mm.

Body length of males (14), 163-M186-213 mm; of females (9), 145-M165-185 mm; tail length of males, 28-M40.5-66 mm; of females, 20-M33.6-42 mm; length of hind foot of males, 22-M27.3-30 mm; of females, 19-M22.1-25 mm.

Condylobasal length of male skull (13), 30.5–M35.3–40.2 mm; of females (9), 29.0–M 32.0–36.8 mm; mastoid width of males, 15.0–M17.3–19.6 mm; of females, 12.8–M15.0–17.5 mm; interorbital width of males, 6.0–M7.7–9.5 mm; of females, 5.0–M6.9–7.0 mm; postorbital width of males, 5.0–M8.2–9.3 mm; of females, 5.3–M7.1–9.0 mm; zygomatic width of males, 11.0–M17.9–22.0 mm; of females, 15.3–M16.2–18.5 mm.

Weight of males 60-100 gm (probably somewhat more).

Middle regions of European part of the USSR from Pribaltic to the middle and southern Urals, northward approximately to the latitude of Leningrad and Perm, and south to Kursk and Voronezh districts.

Outside the USSR—northern parts of Europe, except Finland and northern part of Scandinavian Peninsula.

This form does not possess very definite characteristics and itself represents, on the whole, one of the stages in the transition from the small Siberian and North European form pygmaea to the larger form vulgaris and further to the large southern weasels. The area of intermixing and transition of individuals both toward one (pygmaea) and the other (vulgaris) tendencies, i.e. in the north and in the south, is vast. As was shown, individual animals of the type pygmaea are found to the north of Gorki and Kirov and even Moscow districts, and, at the same time, the weasels of Perm district are already close in dimensions to, or belong to, nivalis. Due to this, individual variation of this form is very great, and equally so with the relatively large "normal" forms, the extreme small variants are found in nearly all of the range of the subspecies and even to Middle and Western Europe (form minuta). Equally with this, individual animals and separate small populations of relatively large weasels are found in the range.

The possibility of accurately diagnosing and designating this form is made more difficult by lack of clarity concerning representation of the typical *nivalis* lineage, which, probably, itself represents a transition from the northern *pygmaea* to the Middle European *vulgaris*. The form *nivalis* is conditionally accepted here.

6. Middle European weasel, M. (M.) n. vulgaris Erxleben, 1777 (syn. nikolskii, dinniki, caucasica, trettaui).

Dimensions somewhat larger than in M. (M.) n. nivalis. Tail relatively longer, its length constitutes on average about 27% of body length and approximately twice as long as the hind foot.

Color of upper body in summer fur varying from light-brownish to dark-chestnut. Winter fur white and only in extreme south of range is whitening incomplete. Hair length on sacrum 7.5–8.5 mm in summer and in winter 10.5–13.5 mm. Skull larger in *M.* (*M.*) *n. nivalis*, and zygomatic arches relatively widely separated.

Body length of males (26), 173-M212.6-243 mm; of females 656 (6), 155-M181.3-212 mm; tail length of males, 45-M57.9-75.5 mm; of females, 45-M54.1-64 mm; length of hind foot of males, 21-M30.8-38 mm; of females, 29-M25.0-31 mm.

Condylobasal length of skull of males, 31.5–M38.8–43.0 mm; of females (6), 25.8–M33.2–36.0 mm; mastoid width of males, 13.5–M18.4–20.5 mm; of females, 14.0–M15.1–16.8 mm; interorbital width of males, 6.5–M8.5–10.2 mm; of females, 6.2–M 7.1–7.5 mm; postorbital width of males, 5.0–M8.4–10.2 mm; of females, 6.0–M7.1–8.0 mm; zygomatic width of males, 17.0–M20.0–22.0 mm.

Southern regions of the European part of the country from the latitude of southern Voronezh and Kursk districts, Crimea, Cis-Caucasus, northern slope of the Main Caucasus, eastward at least to the Volga (eastern border not precisely known).

Outside the USSR—Europe southward to the Alps and Pyrenees.

In some parts of its range in the south, the described form has features significantly similar to large weasels of the type *boccamela*. This reveals itself particularly in the northern Caucasus, and is partially explained by mixing of the population of large Trans-Caucasian weasels penetrating northward, hybridizing with them, etc. An analogous phenomenon is observed in roe deer (see Vol. I of the present series).

The form *vulgaris* in the accepted sense itself represents a transition to the large southern weasels of the type *boccamela*. In the north, the form *vulgaris* insensibly flows together with the form *nivalis* over a broad zone and distinguishing them is only possible through series. The acceptance of two forms is, to a certain degree, conditional.

The majority of western European authors accept for "Germany" the form *trettaui*. This is nothing more than a synonym of the form *vulgaris* and is connected with nothing other than the different nomenclatural interpretations of the name *vulgaris*, believed to be a simple synonym of *nivalis*, a fact which is unfounded. In general, for a correct understanding of the form *nivalis*, a solid revision of the weasels of the Scandinavian Peninsula is necessary. Some authors consider the Scandinavian weasel *M. (M.) n. pygmaea* as identical to the Middle European "*minuta*" and an extreme variant ("minus-variant") of *M. (M.) n. nivalis* (Reichstein, 1957), with which it is difficult to agree.

7. Montane Turkestan weasel, M. (M.) n. pallida Barrett-Hamilton, 1900.

Dimensions somewhat smaller than in M. (M.) n. vulgaris, approximately correspond to dimensions of M. (M.) n. nivalis. Tail of moderate length, constituting about 24% of body length.

Color of summer fur light-brownish. Winter fur white. Skull of moderate size, relatively narrow in mastoid part, postorbital constriction relatively short and narrow.

Body length of males (17), 180-M192-215 mm, tail length, 37-M47-60 mm; length of hind foot, 25-M27-31 mm.

Condylobasal length of the male skull, 31.8–M35.4–40.0 mm; mastoid width, 15.0–M16.6–19.0 mm; interorbital width, 6.5–M7.7–8.4 mm; postorbital width, 6.5–M7.5–8.5 mm; zygomatic width, 18.0–M19.7–22.0 mm.

Weight of males (1), 113 gm, of females (3), 75-108 gm.

*Outside the USSR—found in the Chinese parts of the same mountain systems, and perhaps in extreme eastern parts of Hindukush (Afghanistan).

The scheme presented focuses on the main features and trends in geographic variation of the species in our country. It cannot be considered sufficiently studied, and is not generally accepted (see

^{*}Description of range within USSR omitted in Russian original; this includes montane parts of Turkmenia, Uzbekistan, Tadzhikistan, Kazakhstan, and Kirghizia—Sci. Ed.

Ognev, 1935; Novikov, 1956; Stroganov, 1962). The question of weasels in the European part of the country and Caucasus is particularly complicated.

* * *

For the parts of the range lying outside the USSR, the follow-657 ing forms are usually accepted: 1) M. (M.) n. subpalmata Hemprich et Ehrenberg-Egypt (Lower); 2) M. (M.) n. numidica Pucheran, 1855—Morocco, Algeria, Malta, Azores Islands? Corsica; 3) M. (M.) n. stoliczkana Blanford, 1877—Kashgaria¹⁵; 4) M. (M.) n. siberica Barrett-Hamilton, 1900—Pyrenees [Iberian] Peninsula and Balearic Islands; 5) M. (M.) n. galinthias Bate, 1906—Crete; 6) M. (M.) n. russeliana Thomas, 1911—Sichuan, southern China; 7) M. (M.) n. namiyei Kuroda, 1921—Japanese Islands; 8) M. (M.) n. mosanensis Mori, 1927-Korean Peninsula; 9) M. (M.) n. tonkinensis Bjorkegren, 1942-northern and southern Vietnam (it is probable that this race belongs to another species); 10) M. (M.) n. alleghaniensis Rhoads, 1901¹⁶—southeastern part of the range in America (Michigan, Pennsylvania, Virginia, North Carolina, Ohio, Illinois, Wisconsin); 11) M. (M.) n. campestris Jackson, 1913—southwestern angle of the range in America (South Dakota, Iowa, Nebraska); 12) M. (M.) n. eskimo Stone, 1900—Alaska; 13) M. (M.) n. rixosa Bangs, 1896—remaining major part of the range in America (Mackenzie, Labrador, Ouebec, Minnesota, North Dakota, Montana, Saskatchewan, Alberta, British Columbia) (V.H.).

Biology

Population. Within the boundaries of its range, the weasel is everywhere quite common, but unevenly distributed, animal. This small carnivore serves as a good indicator of the abundance of mouse-like rodents—almost its sole food. At the same time, wherever ermine are abundant, weasels are few and vice versa (Ognev, 1931). This applies to the distribution of both numbers

¹⁵Information about the existence of this form in the USSR in Semirech'e at Dzharkent (Ellermann and Morrison-Scott, 1951) with reference to Ognev (apparently 1935), is based on misunderstanding. In describing this form, S.I. Ognev nowhere spoke about its presence within the boundary of the USSR and refers to Yarkend (Kashgaria) and not Dzharkent* (Semirech'e).

*Now Panfilov-Sci. Ed.

 16 The American authors consider this and the following form as belonging to a separate species M. (M.) rixosa.

inside the range and density in separate stations at the limits of the area. In the upper Pechora, one weasel track is found for 10–18 tracks of ermine; on the contrary, in the southwestern part of Kalinin district, 3–4 tracks of weasel for 1 track of ermine, and in Zhiguli, 7 weasel tracks for 1 ermine.

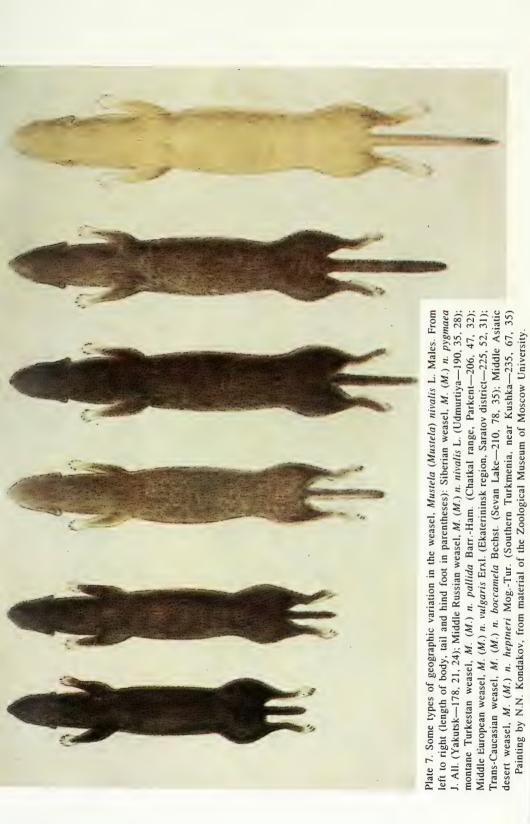
The area of weasel abundance lies more southward than that of ermine, and numbers of ermine in southern regions is usually less than weasel numbers. This partly depends on differences in possibilities of capture of mouse-like rodents between these two species. In the European part of the USSR, weasels are found in small numbers in the taiga forest zone. In this zone, they mainly live in fields and around human settlements, and are rare in the forests. In the intermediate zone, it decidedly predominates over the ermine. This is still more obvious in the forest-steppe belt and the chernozem steppes. In the Caucasus, the weasel completely predominates. In Siberia, it is more numerous in the southern parts. In northeastern Siberia, it is rare. It is more often encountered in southern Trans-Baikal and Primore Territory.

Due to significant fluctuations in numbers, moreover not onetime, its occurrence in different parts of its range can only be compared under similarly favorable environmental conditions. Table 62 gives the frequency of weasel tracks (per 10 km) for the mixed forest zone and for broad-leaf forests. Extreme magnitudes apply to different habitats in one season. In both cases, frequency of tracks may change 8–10-fold, but in all cases, in broad-leaf forests, it is 3–4 times more than in mixed forests.

Habitat. The weasel is not finicky, and can accommodate itself easily to any conditions. Wherever there are many mouse-like rodents, one may find the weasel. It is established in tundra, does not avoid taiga and is common in the forest-steppe zone and chernozem steppes. It lives in grassy steppes, semideserts and mountains. It does not avoid proximity to humans, settling sometimes in

Table 62. Frequency of weasel tracks in the broad-leaf [Zhiguli] and mixed forests [Kalinin] (along 10 km route)

Region	Year of high	numbers	Year of lo	w numbers
	Quantity			
	Extreme	Average	Extreme	Average
Southwestern part, Kalinin district	0.7-12.8	9.7	0.2-8.6	0.9
Zhiguli	9.7-122.8	36.2	0-13.3	2.7





structures within a town (outskirts of Moscow). Although encountered almost everywhere, the weasel is known to prefer certain places. Thus, in the middle forest belt, the weasel is most often met with in openings, clearings, forest edges, plantations, roadside ditches, etc. It is often in riparian vegetation of small rivulets, in meadows with haystacks, in mezha*, threshing-floors**, in storehouses, barns, and other buildings in villages. In Siberia, the weasel is more often encountered in steppe than in taiga, where it mainly restricts itself to meadows, old burns and in tall grass. In the chernozem and steppe belts, it inhabits steppes, fields, pastures, gardens, vegetable gardens, stonepiles, woodpiles, threshing-floor**, hay/grain stacks, fences, inhabited and uninhabited structures; and in mountainous places—among talus slopes, boulder fields, etc. In deserts and semideserts, the weasel is closely associated with the places where colonies of social rodents are found, mainly gerbils (particularly great gerbil [Rhombomys opimus]) and simply lives among these colonies or in them (V.G. Heptner).

Food. The weasel basically feeds on mouse-like rodents: voles, mice, hamsters, gerbils and others. Food composition is variable, and depends upon which of them predominates in the given locality. The weasel does not always decide to attack adult hamsters and rats. The weasel usually bites small voles in the occipital region of the skull. This is the only way it kills its prey. It can bite through [the skull of] a young water vole only with difficulty; it can deal with pikas and gerbils, but it cannot overcome young Norway rats and sousliks.

Species composition of prey is also determined by habitat of the weasel—in the same locality, it behaves different in forest than near villages and in the fields. A characteristic feature of the weasel is the fact that in its food, shrews are more numerous than in other carnivores (Formozov, 1948); in different years in Tatariya, their frequency reaches 25% (Grigor'ev and Teplov, 1939).

In Murmansk district, the diet of the weasel consists of gray [Microtus] and red-backed [Clethrionomys] voles, Norway [Lemmus] and wood [Myopus] lemmings, and rarely fish

^{*}Strip of uncultivated land between two fields-Sci. Ed.

^{**}Two Russian words, tok and gumno, are both translated as "threshing-floor"—Sci. Ed.

(Nasimovich, 1948). In Trans-Baikal, the weasel feeds on narrowskulled voles [M. gregalis] (50%), Asiatic wood mice [Apodemus peninsulae] (25%), bank voles [C. glareolus] (12.5%) and small birds (12.5%) (Fetisov, 1942). In the steppes of the northern parts of the Mongolian Republic, in years with an abundance of Brandt's vole [Lasiopodomys brandti], the weasel feeds mainly on it as well as on the clawed Mongolian gerbil [Meriones unguiculatus] (Kucheruk, 1948); in the deserts of Pri-Balkhash—on the great gerbil [Rhombomys] (Sludskii, 1953). In the forest-steppe of western Siberia, small voles, field mice, Dzhungarian hamsters, 659 [Phodopus sungorus], water voles enter the weasel diet, and in small amounts, water voles and fish, and even carrion is sometimes met with (9.1%; Zverev, 1931). In Tatariya, the common vole predominates (23.1%) in the weasel diet, while other voles, including water, and field mice, are utilized in lesser quantity. The average percentage of occurrence of brown-toothed shrews [Sorex] equals 17% (Grigor'ev and Teplov, 1939). In the middle [forest] belt, the weasel prefers the common vole and field mice. In captivity, water shrews [Neomys] are very unwillingly utilized (V.V. Kucheruk). Frogs, fish, small birds and bird eggs are very rare in weasel food. In Ussuri Territory, the weasel often eats terrestrial molluses and feeds on a number of marine organisms cast up on the seashore (Yu.A. Salmin and V.O. Shamykin).

In the literature are known cases of successful attack by weasels on larger prey-larger than the weasel itself-up to capercaillie, hazelhen and hare. However, such cases occur extremely rarely. In the stomachs of weasels are the remains, at one time of only one mouse-like rodent; in it usually occur no more than 10 gm of food (Griror'ev and Teplov, 1939), a weight constituting about 1/10 of the weasel's body weight. The daily [food] norm of the little animal is equal to about 35 gm, i.e. about 30-35% of its body weight (V.V. Kucheruk). However, weasel kills significantly more mouse-like rodents and shrews than needed for food. When its prey is found in abundance, it eats only a small part of captured animal, sometimes only the brain. According to the method of obtaining its food, the large Caucasian weasels undoubtedly belong to the ermine type, since it is impossible for them to penetrate into the holes of small rodents because of their large dimensions.

Home range: The dimensions of the weasel's home range are determined by the abundance of the prey within its limits, and the



659 Fig. 238. Turkmenian weasel, *Mustela (Mustela) nivalis heptneri* L. Tur*., looking out from a burrow of a great gerbil, *Rhombomys opimus*. Kyzyl-Dzhar in Badkhyz preserve, southern Turkmeniya. 28 April 1963. Photograph by Yu.K. Gorelov.

daily range depend also on weather conditions. The home range is usually distributed among a series of adjacent areas of daily activity. The home ranges of males and females for the most part occur contiguously. In the forest-steppe of western Siberia, the area of daily activity sometimes comprises 0.5–0.6 ha (Zverev, 1931). In Murmansk district, the dimensions of the home range of weasels in winter did not exceed 10 hectares in many cases. The length of the daily route in this case ranged from 1.5–2.5 km (Nasimovich, 1949).

Burrows and shelters. In winter, the weasel has no permanent burrows or other shelters. In Murmansk district, when at rest, it always lies beneath the protection of the snow—in the roots of a spruce tree, among stones, and under fallen branches (Nasimovich, 1948). In the middle [forest] zone, these occur as woodpiles, heaps of brushwood or fallen branches, straw stacks or piles of hay in

^{*} In Russian original, misspelled "Tep"., but author of name, *heptneri* is Morosova Turova; see p.—Sci. Ed.

meadows; and finally, quite often, the subnival nest of a vole which the weasel has eaten (Tikhvinskii, 1936). Usually within the limits of the home range, the weasel has some shelters which it regularly visits.

There is little reliable data on brood burrows. There are indications that nests of weasel with broods were sometimes found under old rotten stumps or among sheaves and straw remains of the previous year. The weasel often settles with its brood in nesting chambers of vole burrows.

Daily activity and behavior. The weasel has no defined regime of daily activity. It is, for the most part, active at twilight and at night, but it or its fresh tracks may be met during daytime, especially during a snowfall or snowstorm.

In case of food abundance, the area of daily activity is densely covered with its tracks in a very small area. At night, it does not pass by any fallen log, bush, stump, hole, or heap of branches without inspection. When its prey is scarce, the tracks of the weasel



660 Fig. 239. Turkmenian weasel, hunting in a colony of great gerbil. Kyzyl-Dzhar in Badkhyz reserve, southern Turkmeniya. A steppe agama is between the teeth of the weasel. 26 April 1963. Photograph by Yu.K. Gorelov.

extend along an almost straight line for hundreds of steps to another more prey-rich area. The weasel usually hides for a long period in subnival burrows of voles and shrews. Very often, it uses the underground passages of moles. In severe frost or crusted snow, the weasel almost never appears on the snow surface. It almost always catches its prey under the snow and rarely on its surface.

The weasel moves exclusively by jumps, with the distance between tracks of the fore and hind feet from 18–35 cm, depending on the leap and the size of the animal. In Middle Russia, length of the leap is 18–20 cm, the feet stand close in the leap. Given the possibility of killing mice and voles in excess of its daily needs, the weasel often makes stores, sometimes very significant, and usually in one place, where from 1 to 19 voles and mice may be found. In 13 cases, their average number was 8 (V.V. Kucheruk).

Reproduction. Reliable data on the time of mating and the duration of the rut period are lacking. There are also no data on the duration of pregnancy, as well as on its nature. To all appearances, all stages in the reproductive cycle of the weasel, except possibly the duration of pregnancy (from the moment of placentation to parturition) are inconstant and variable. They are determined by factors of the external environment, and first of all by food abundance.

In Silesia, pregnant females were found in January, April, August, October and November (Pohle, 1909); in the Caucasus in April, May and October (Satunin, 1915). In southeastern Trans-Baikal, pregnant females as well as those which had just given birth to young were simultaneously found at the end of June and the end of July (P.B. Yurgenson). In Kostromsk district, a female with five fetuses was caught in spring (Formozov, 1948). In Tatariya, two nursing females were caught on 7 April and 1 May, and two pregnant ones on 2 and 5 May. The nursing females had 4-6 placental scars and in the pregnant ones, the same number of embryos were found (V.A. Popov). On 14 April, a nursing female was caught (V.V. Kucheruk). In Kazakhstan, pregnant and post-partum females were found in May (Sludskii, 1953), and in northern Kirghizia, young weasels had almost reached adult size by the end of June (Kuznetsov, 1948). According to data of the Kazan Zoo (1929), the minimal duration of pregnancy was 7-8 weeks. Thus, pregnant females were found in various parts of the range in all months of the year, but more frequently in spring, in April. Young were caught in March, May, June, July, November and December, and in the German Democratic Republic and the Federal Republic of Germany, also in September and January.

Most often, litters of 4 to 7 young occur, rarely were 3, 8 or 9 observed. There is a written record of 10 young found in a burrow (Novikov, 1959). The number of males in litter is usually more than that of females. The number of young in the litter depends on abundance of food in the given season. In years with abundant mouse-like rodents in the Mongolian Republic, there were significantly more embryos (11, 11, 15, 16) than were found in years of their depression (5, 7). The maximum known number of embryos is 19 (V.V. Kucheruk).

Growth, development, and molt. Weasels are born blind, helpless, covered with scarce whitish underfur. They stay with the mother for a long time. The brood disperses at the end of summer or in autumn, when the young are already comparable in size to the mother.

Molting proceeds twice per year—in spring and in autumn.

Enemies, diseases, parasites, mortality, and competitors. All carnivorous animals and birds feeding on mouse-like rodents, and first of all the ermine, are competitors of the weasel. Many of these are, at the same time, enemies of the weasel, destroying it. Remains of eaten weasels occur in excrement and debris of red fox, sable, steppe and forest polecats, ermine, eagle-owl, buzzard and others. Such cases are rare, but nevertheless occur in places.

Diseases of weasels are almost unstudied. There is some information that the weasel is susceptible to rodent plague; a culture of tularemia infection was isolated from it, but the weasel is quite resistant to tularemia (Olsuf'ev and Dunaeva, 1951). Skryabingilosis is widespread among weasels, as also in ermine.

Rates of mortality and longevity have not been studied. Undoubtedly, in years of sharp decrease in numbers of mouse-like rodents, many weasels die from hunger.

Population dynamics. Fluctuations in numbers of weasels is well-demonstrated. They are very closely connected with the abundance of food—mouse-like rodents—not of only one species, but of the whole number of small mammals (voles, mice, shrews; Formozov, 1948). In a series of cases, as in the majority of the carnivorous animals, its population apparently increases in the year following one of food abundance (Migulin, 1941; Formozov, 1948).

and others). But this does not always occur. Thus, in southeastern Trans-Baikal, in 1939-1950, the weasel population increased simultaneously with growth in the abundance of mouse-like rodents. The same was observed in the southwestern part of Kalinin district in 1948-1950 (P.B. Yurgenson). This may be explained by the unstable and prolonged period of reproduction of the animal. In southeastern Trans-Baikal, within a nine-year period, the number of weasels rose three times (P.B. Yurgenson). In Kostromsk district, over a 10-summer period, it was observed that the number of weasels regularly increased every other year (Formozov, 1948); after a year of abundance, numbers fell sharply the following year. Rapid increase in numbers is explained by high fertility, and sharp fluctuations—by narrow feeding specialization (voles and shrews). In southeastern Trans-Baikal, within a nine-year period the number of weasels changed by 2-3-fold (P.B. Yurgenson). In the Mongolian Republic, between 1944-45, there was noted a nine-fold increase in number of weasels (Kucheruk, 1948). In May 1944, in one hectare of the test areas, an average of 0.14 weasel was obtained; in June—0.66; in September—1.27 weasels. In April 1945, no weasels were caught in any of the test areas. In Kostromsk district, during one year the weasel population increased and decreased 10-fold (Formozov, 1948). During the period from 1930 to 1950, the weasel population in the southwestern part of Kalinin district changed 34-fold (1934/35 and 1947/48; P.B. Yurgenson), and in the year following the end of the war, occurrences were very low—0.28-0.58/10 km route. In the upper Pechora, a 25 [fold] short-term fluctuation of the weasel population was observed (Teploy, 1951).

Field characteristics. It is very easy to confuse the track of a large male weasel with those of a small female ermine. In such cases, the weasel is distinguished by its considerably smaller area of daily activity, the shorter daily length of the trail and also the very uneven restless movement in short (5–10 m) wave-like zigzags, while in ermine, the angles of turning are more acute (Nasimovich, 1949). In walking, ermine sometimes "trot", which in weasels has never been observed. The weasel places its feet closer to each other than ermine, and in short jumps the tracks of "landing" and "bounding up" often join in one chain. The length of leaps of weasels in the eastern Altai (Dul'keit, 1956) is 15–25 cm, the



Fig. 240. Paired foot impressions of male Middle Russian weasel, *Mustela (Mustela) nivalis* L., on snow and the pattern of leaps during quick movement of the animal. Fomkino, Moscow district. 8 December 1963. Sketch by A.N. Formozov, nat. size.



Fig. 241. A group of tracks of the Middle Russian weasel, jumping easily on four legs on the first snow. Fomkino, Moscow district. 15 November 1951. Sketch by A.N. Formozov, about 2/3 nat. size.

diameter of the individual track is 1.0–1.6 cm (in ermine, 1.8–2.5). The weasel sinks into the snow for about 1.5–2.5 cm. The weight load on 1 cm² of the surface of the track is 7–8 gm (P.Yu.).

Practical Significance

The significance of the weasel in the destruction of harmful mouse-like rodents is very great. This is, in particular, strengthened by the fact that, in years of abundance, it kills tens and hundreds of times more rodents than it can eat. According to some data, a weasel can kill up to 2000–3000 rodents in a year. In "eating places" of the weasel, up to 456 half-eaten voles and mice were found among the stacks of straw on the threshing floor. The weasel hunts rodents not only in fields and forests, but also in the villages—in hay piles of straw stacks, storehouses and store-rooms. Almost everywhere, where mice and vole can penetrate, the weasel can also.

In the fur trade, the role of weasel is negligible. It is only accidentally captured in traps set for ermine, Siberian weasel, etc. The weasel fairly often gets into traps placed for moles. In a year of abundant weasels, one weasel was caught against 25–40 moles (Formozov, 1948).

As a destroyer of harmful rodents, the weasel must be protected and preserved throughout the year, and its hunting must be prohibited everywhere. Its trade should be everywhere prohibited, and the accidentally captured weasel must not be used in fur preparation to avoid encouraging its hunting (P.Yu.).

ERMINE

Mustela (Mustela) erminea Linnaeus, 1758

- 1758. Mustela erminea. Linnaeus. Syst. Naturae, ed. X, 1, p. 46. Sweden.
- 1792. Mustela erminea aestiva. Kerr. Animal Kingdom, p. 181. Germany.
- 1816. *Mustela herminea*. Oken. Lehrb. Naturg. 3, 2, p. 1026. Renaming of *erminea* Linnaeus.
- 1857. Putorius kaneii. Baird. Mammals North Amer., p. 172. Arikam Island in Bering Sea. Apparently, Arakamchechen Island (V.H.).

- 1895. Putorius ermineus ferghanae. Thomas. Ann. Mag. Nat. Hist., 15, p. 452. Kara-Karyk mountains, Fergana. (?V.G.).
- 1896. Putorius arcticus. Merriam. North Amer. Fauna, 11, p. 15. Point Barrow, Alaska.
- 1912. *Mustela lymani*. Hollister. Smiths. Misc. Coll., 60, 14, p. 5. Tapucha*, on the Chuisk Trail, southern Altai.
- 1913. Mustela nippon. Cabrera. Biol. Soc. Espan., 13, p. 392. Sinano, on Hondo (Honshu) Island, Japan.
- 1914. *Mustela kanei*. G. Allen. Proc. New Engl. Zool. Club, 5, p. 58. Nizhne-Kolymsk.
- 1922. Putorius erminea var. kamstschatica. Dybowski. Arch. Tow. Nauk. Lwow, 1, p. 349. Nom. nudum.
- 1922. Putorius erminea var. sibirica. Dybowski. Ibidem, p. 349. Nom. nudum. Nec Pallas, 1773.
- 1923. Arctogale erminea tobolica. Ognev. Biologich. izvestiya, I, p. 112. Tara, Former Tobol'sk governance.
- 1928. Mustela erminea transbaikalica. Ognev. Memuary zool. otd. Obshch. lyubit. estestvozn., antrop. i etnogr., 2. Sosnovka, Barguzinsk Preserve.
- 1928. Mustela erminea orientalis. Ognev. Ibidem, p. 15. Pokhodskoe S. [village] on the Kolyma [river], 69°04′ N. lat., 160°55′ E. long.
- 1929. Mustela erminea baturini. Ognev. Izv. Tikhookeanskoi nauchno-prom. stantsii, 2, No. 5, p. 9. Great Shantar Island in Okhotsk Sea, lower Anaur river.
 - 1931. Mustela erminea birulai. Martino. Ezhegodn. Zool. muzeya AN SSSR, 31, 1930, p. 208. Aktyubinsk. Nomen praeoccupatum—Kolonokus alpinus birulai Ogn., 1928.
 - 1932. Mustela erminea ognevi. Jurgenson. Zool. Anz., 98, p. 11. Mouth of Taz river, western Siberia.
 - 1935. Mustela erminea schnitnikovi. Ognev. Zveri SSSR i prilezhashchikh stran, 3, p. 37. Former Kopal'sk Co., Semirechensk governance.
 - 1936. Mustela erminea karaginensis. Jurgenson. Byull. Mosk. Obshch. ispyt. prirody, 45, No. 3, p. 240. Karaginsk Island near eastern shore of Kamchatka.
 - 1938. Mustela erminea naumovi. Jurgenson. Tr. Altaiskovo gos. zapovednik, 1, p. 124. Voevoli Lake, source of Khatanga, 66° N. lat.

^{*}In Russian original, misspelled Topuchaya-Sci. Ed.

- 1941. (1939). *Mustela erminea teberdina*. Kornejev. Acta Mus. Zool. Kijev, 1, p. 174. Teberdinsk Preserve, Caucasus.
- 1944. Mustela erminea digna Hall. Proc. Calif. Acad. Sc., 23, No. 37, p. 559. Kamchatka.
- 1951. Mustela erminea martinoi. Ellerman et Morrison-Scott. Checklist Palaearct. Indian Mamm., p. 256. Substitute for M. e. birulai Martino.
- 1962. Mustela erminea balkarica. Baziev. Zool. Zhurn., 41, No. 1, p. 123. Chegem river gorge, northern slope of Great Caucasus (V.H.).

Diagnosis

Color monotone white or dark-brownish tone above and white below, with dorsal and ventral colors sharply demarcated. Distal half of tail black. Tail length with terminal hairs comprises about half to more than a third of body length. Skull moderately elongated—distance between the mastoid processes approximately equal to half of condylobasal length, but somewhat more elongated than in weasel. Width of skull above canines noteably less than interorbital space. Dimensions are small (V.H.).

Description

In its general proportions, manner of posture and movement, the ermine is entirely similar to the weasel and represents a somewhat enlarged copy of it. However, the tail is relatively longer, never being equal to the length of the hind foot, always exceeding a third of body length, and its length together with terminal hairs constitutes about half of body length.

Winter fur very dense and silky, but quite closely-lying and short; summer fur rougher, shorter and sparse. Among ermine around Moscow, length of directional hairs in winter is up to 17 mm (M15.75), and in summer, M13.9; guard hairs of category I in winter to 15 mm (M13.7), and in summer, M12.1; guard hairs in category II in winter to 14 mm (M12.2), in summer M11.3; guard hairs in category III in winter to 13 mm (M11.9), in summer M10.5; guard hairs in category IV to 12 mm (M11.5), in summer M9.9; length of underfur in winter M9.1 mm, in summer 8.1. The total number of hairs in 0.25 cm² in winter comprises 4808, of

which two* are directional hairs while underfur hairs number 4,637—1 for every 27 underhairs; in summer, on 0.25 cm², there are 3,636 hairs, of which there are 5 directional hairs and underhairs number 3,539—1 for every 36.5 underhairs. Thickness of fur of ermine in summer decreases by 25% while in the majority of species, it decreases by about two times (Pavlova, 1959). Difference in character of winter and summer fur in southernmost forms is less than in northern. The tail is covered by short closely-lying hairs, not fluffy, and relatively fine and even throughout whole length of the tail.

Soles of feet furred and in winter fur, their pads are not visible. In summer, pelage is less dense and pads are bared.

In summer color is two-toned—on the dorsal side of the body, the top of the head and the sides are brownish in color of various densities and tones; the underside, the inner sides of the feet and the lower part of the neck and head are white with greater or lesser yellowish or lemon-yellow film; in extreme cases, the belly is quite bright yellow. The distal half of the tail is black in winter and in



Fig. 242. Ermine, Mustela (Mustela) erminea L., in summer fur. Sketch by A.N. Komarov.

*Sic; this number may be in error—Sci. Ed.

summer, the upper and lower parts of the basal half correspond with the color of the back. The dorsal surface of the feet of both fore and hind legs are white or yellowish-white.

Individual variation in color is not great. There are no age or sexual differences in color. Geographic variation in color of the summer fur is noticeably expressed, but is not great; color changes from dark-tawny and dark-brown to quite light straw-brown. Geographic variation in color of the winter fur is not expressed. As noted, seasonal variation is great and expressed in all races. Only a few of the southernmost populations or individual animals in these populations do not turn white or partially white in winter.

The ermine skull is very similar to that of weasel, but relatively more elongated, with a less broad and swollen braincase. Its anterior region (in the region of the frontal bones) is not so wide and voluminous and is more elongated. The postorbital constriction is sharper and somewhat longer. The facial portion of the skull is elongated and relatively narrow—skull width above the canines is notably less than width of the interorbital expanse. The zygomatic arches are weak and thin. Zygomatic width approximately corresponds with skull width in the mastoid region. The infraorbital foramina are rounded and relatively large—their transverse diameter is considerably larger than the longitudinal diameter of the canine alveolus.

The upper profile of the skull in the region posterior to the supraorbital processes is flattened, and therefore in the interorbital 667 region, there is an evident elevation, from which the profile of the facial part quite abruptly descends. The prominences, crests, etc. are weakly defined, but relatively somewhat stronger than in weasel—the better defined is the sagittal crest found in the postorbital (frontal) region, and the occipital crest is well defined. The auditory capsules are narrow and high, their inner edges parallel to each other. The distance between them is less than in weasel, being less wide than the hard palate at the level of the anterior edge of the sphenopalatine notch. Teeth are small, but relatively somewhat stronger than in weasel. Carnassial teeth are well developed, the upper canines longer and thinner and the lower canines somewhat massive.

On the whole, because of its relative elongation, less swollen braincase and its flatness, elongation of facial part, development of crest, prominences, etc., the ermine skull has a less "infantile"

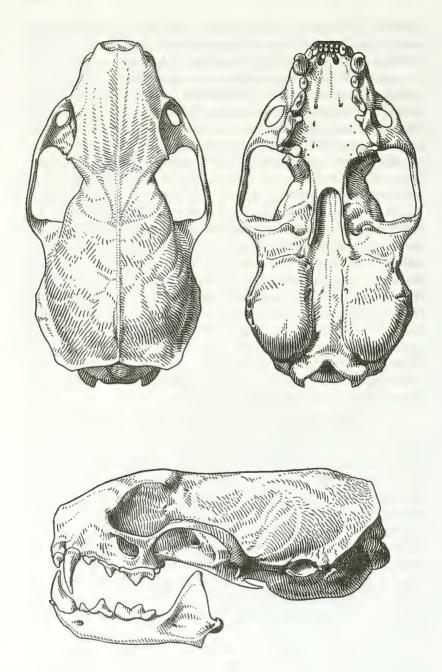


Fig. 243. Skull of ermine, Mustela (Mustela) erminea L.

character than the weasel skull. This applies both to the larger and the smaller races of the species.

Age changes in the ermine skull are quite considerable.¹⁷ The young ermine skull (first winter of life), besides somewhat smaller general dimensions, is distinguished by a relatively short facial part, rounded and somewhat swollen braincase, weak supraorbital processes and shorter postorbital constriction. The pace of age changes in the skull is quite rapid, and in the second winter of its life, the animal has a skull which cannot be differentiated from that of adults in its main features (for age changes, see also description of the os penis).

Sexual differences are considerable and are manifested in its somewhat different proportions of the female skull besides its generally smaller dimensions. In females, the skull is somewhat narrower in the nasal part (about 23.3% of condylobasal length against 24.1% on average in males), mastoid width is somewhat less (about 54% against 55.7% on average in males), in females, the facial part is shorter (about 45.5% against 48.7% in males), the cranium is relatively somewhat longer (59.2% against 55.3%). Crests in females are usually not defined, occurring only in old individuals, and even so are relatively less than in males (Morozova-Turova, 1961). The female skull is not so massive and is absolutely and on average lighter. The weight of male skulls (120) without lower jaws from Kamsko-Bel'sk flood lands is 1.9–M2.47–2.7 gm; that of females (70) is 1.3–M1.54–1.9 gm. The comparative weight of the male skull is 165% of that of the female skull.

Condylobasal length of the male skull (the same series) is 45.5–M48.39–51.8 mm, that of females is 40.3–M43.39–45.8 mm (V. Popov, 1947).

Extent of individual variation in skulls is quite considerable in general, particularly in characters of general size; however, this variability is of "normal" character and does not attain the amplitude found in some especially variable races of weasel. Zygomatic width is strongly variable, width of skull above canines, and particularly in the postorbital constriction which may be longer and wider or shorter, sharper or weaker. All of this leads to the

¹⁷Age and sexual variation in the ermine skull was the subject of several special investigations; it was better studied than other species of the family. It serves, to a certain degree, as a model for the genus. Very general information is given here. For details, see Yurgenson, 1933; Stroganov, 1937; V. Popov, 1943, 1947; O. Petrov, 1951; Morozova-Turova, 1961.

fact that skulls within one race may be more elongated or wider and, in general, obviously differ in their general appearance. This has repeatedly led to misunderstandings in description of separate forms. Geographic variation of the ermine skull is insignificant, much less than in weasel, and these differences are never so great. Geographical changes are not of the degree seen in sexual dimorphism.

668

The os penis differs from the corresponding bone of other species of the genus in that its anterior end is not curved upwards in the form of a hook, and it has a greatly elongated S-shape form. The base of the bone is swollen, with a rough surface, and the anterior end is broadened, with a narrow spoon-shaped depression. A narrow groove extends along the lower surface of the distal half. Age differences in the structure and dimensions of the bone are considerable. In adults (sexually mature), it is larger and heavier. In adult ermines of Volzhsk-Kamsk territory, its length is 23.7–M25.5–27.7 mm; weight is 0.033–M0.041–0.048 gm; in immature (young and subadult) its length is 22.2–M23.5–24.3 mm, weight is 0.016–M0.025–0.32 gm (V. Popov, 1947).

Dimensions of ermine are variable; however, this variability is "normal", and its extent is not so great as in the weasel. Body length of males (75) is 187–325 mm, of females (47), 170–270 mm; tail length of males is 75–120 mm, of females, 65–106 mm; length of hind foot of males is 40.0–48.2 mm, of females, 37.0–47.6 mm; height of ear in males is 18.0–23.2 mm, of females, 14.0–23.3 mm.

Condylobasal length of male skull (213), 39.3–52.2 mm, of females 35.7–45.8 mm; zygomatic width of males 21.0–30.6 mm, of females 18.2–24.2 mm; interorbital width of males 9.1–13.2 mm, of females 7.9–10.9 mm; mastoid width of males 19.1–26.3 mm, of females 16.8–21.7 mm.

Weight of males to 258 gm, of females to 180 gm, usually much less 18 (V.H.).

¹⁸According to Stroganov (1962) data for ermine of our country. They also characterize ermine of West Europe. Here, only individual animals (judging from a large series; Reichstein, 1957) with perhaps slightly larger measurements (interorbital width of males 13.7, females 11.8 mm; zygomatic width of females 24.6). The given amplitude and dimensions also applies to the small form of ermine from the highlands of the western and central Alps (*M. e. minima*). Some measurements given by Novikov (1956) are not fully accurate (body length 160–380 mm, one condylobasal length of females 47 mm and others). American ermine may be somewhat larger than European (body length of males 235–340 mm, females 190–290 mm: Hall and Kelson, 1959).

Systematic Position

The relationship of ermine to affiliated species of the genus was reviewed in the description of weasel (see above) and *M. altaica* (see below), with which this species is closely related. The most fundamental difference lies in the structure of the os penis which is apparently, important in a biological sense. In contrast to weasel, the ermine must be considered as a more "specialized" or rather "advanced" form, although the weakening of "infantile" features characteristic of weasel, are probably connected primarily to larger general measurements of ermine (allometry). The placing of ermine at the beginning of the entire series of species of the genus, as is usually done, has no foundation (V.H.).

Geographic Distribution

Arctic and boreal zones of the Old and New Worlds.

Geographic Range in the Soviet Union

This represents the basic and greatest part of the species range and occupies the major part of the territory of the USSR.

The northern border of the range constitutes the coast of the Arctic Ocean, to which the ermine reaches even in the northern Taimyr, i.e. to 77° N. lat. It is also encountered on the small islands near the mainland—in the southern part of the Kara Sea on the Shokal'sk, Olen'em, Sibiryakova, and Dixon islands, and probably Beloi, Nordenskiold; in the Laptev Sea-on Begichev and Salkai islands and islands of the Lena delta. It is known from Bol'shoi Lyakhovsk and Kotel'noe and, apparently, is found in other islands of the Novosibirsk archipelago. It is absent on the 670 remaining islands of the Arctic (occurrence on Baigach is entirely possible). In the east, the border of the range passes along the Bering, Okhotsk and Japanese seacoasts and inhabits Karagin Island, two of the northern Kuril Islands (Paramushir and Shumshu) and from the South Kunashir. Communications on its occurrence on Iturup (Klumov, 1962)—not confirmed by new data (V.G. Voronov). It is encountered on Sakhalin and all of the Shantar Islands.

The western frontier, from the Barents Sea to the Black Sea, forms the western border.

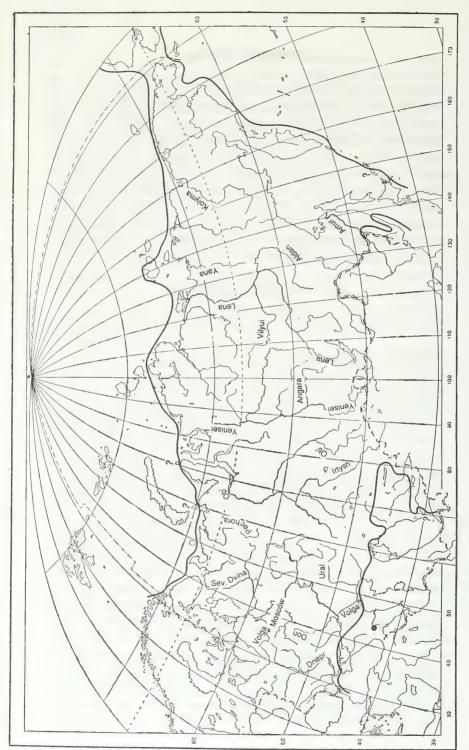


Fig. 244. Borders of distribution of ermine, Mustela (Mustela) erminea L., in the USSR. V.G. Heptner.

The southern border of the range in the European part of the USSR and in Kazakhstan extends into the steppe and semidesert, and in part even the desert zone. In the west, between the state frontier and the mouth of the Dnepr, the ermine is met with up to the Black Sea coast and is found even on Tendrov Spit. The ermine is absent on the Crimean Peninsula (information of Kalenichenko, 1839, is erroneous) and eastwards from the Dnepr in the narrow steppe belt, which is directly adjacent to the Black and Azov seas. It exists immediately around Askaniya Nova and at the mouth of the Don, and perhaps, even below Taganrog and along the northern shore of Taganrog Gulf of the Azov Sea. Farther to the east, the ermine is quite common in the delta of the Volga, is also found farther to the southwest (Mikhailovka, former Birvuche-Kosinsk region, Yasta) and, apparently, is encountered along the Kuma, at least at its mouth. However, there are no precise data on the southern limit of the ermine's range in the steppes of the Cis-Caucasus and at the present moment the boundary to a significant extent is conditionally accepted as passing from the mouth of the Don to the mouth of the Kuma.

Ermine exists in the Main Caucasus in the El'brus massif, where it is recorded from a series of places from the source of the Baksan to the source of the Cherek (Kabardino-Balkhariya) to a height of from 2,500 to 3,200 m above sea level, in Teberda preserve¹⁹. The inhabited region in Kabarda is, apparently, cut off from the general range of the species.

From the mouth of the Volga, the boundary passes eastward along the coast of the Caspian Sea to the mouths of the Ural and Emba and even somewhat farther south. Thence, extending around the northern Chink of the Ustyurt from the north, the southern boundary of the range extends to the northwestern shore of the Aral Sea, continues along its northern shore including Aral'sk

¹⁹Data of Korneev (1941), Tembotov (1960) and Basiev (1962). Ermine was discovered credibly in Teberda in 1934 (Korneev, 194) and Kabardino-Balkariya only in 1959 by V. Dmitriev. Up to the end of 1961, 4 individuals only had been trapped. Earlier, the only known data were those of Satunin (1915) about the capture of animal in the El'brus in the beginning of the century. Later, when this finding did not receive confirmation, the occurrence of ermine in the Caucasus was rejected or at least not confirmed. The fact that all data found in the monograph of Vereshchagin (1959), even those concerning the mouth of the Kuma, were placed in doubt is of some significance for the general problem of the ermine in Caucasus in the last decade since its absence was not accepted either. Up to the present time the ermine has not been found in the Caucasus preserve, although it apparently lives there.

Karakum and extends a tongue to the south that includes the lower Syr'-Dar'ya and descends as far as Kzyl-Orda. Thence, the boundary abruptly ascends to the north, passing through the southern foothills of the Ulutau, traverses the Sarysu, nearly in its middle course and goes on to the Kyzylrai mountains (a little north of the mid-part of [Lake] Balkhash, 75° E. long.) passing around them from the south as well as Ayaguz (Sergiopol'). From there the border line turns southwards to the western part of the Alakul'sk depression, leaving it at the range boundary.

The range in Middle Asia may be outlined in the following form. In the desert lowlands and sands south of [Lake] Balkhash and along the rivers flow into the lake, the ermine is absent. It exists in the expanse between Alakol' and Dzhungarsk Alatau and in this system, between the Dzhungarsk Alatau and Zailiisk Alatau and along the entire Tien Shan system to its western extremity, including the Kirghiz (Aleksandrov) range and, probably, Talas Alatau. Ermine is absent in the Karatau.

The species described is found in Fergana and in the Pamiro-Alaisk system. Details about its distribution here are almost absent. Apparently, however, the ermine occupies the whole Pamir, Zaalaisk and Darvazsk ranges, and probably Peter the Great range. Concerning the Gissar, Zeravshan and Turkestan ranges, there are no data. Apparently, ermine does not occur south of Tadzhikistan in the region of low desert mountains. Eastward in Middle Asia, the ermine is everywhere distributed to the state frontier.²⁰

Throughout the distance from the Alakul depression all the way to the mouth of the Ussuri, the range extends southwards to the state frontier and beyond it. Beside, it is possible that ermine is absent in the Amur Valley and adjacent places between the mouths of the Sungar and Khabarovsk.

In Ussuri Territory, the ermine is absent in the western part along the Ussuri and the lower courses of its tributaries, and along the coastal zone northwards to a region somewhat north of the

²⁰Range according to data of Kalenichenko, 1839; A.M. Nikol'skii, 1891; Byalynitskii-Biruli, 1907; Dinnik, 1914; Satunin, 1915; Orlov and Fenyuk, 1927; Adlerberg, 1935; Ognev, 1935; Rozanov, 1935; Flerov, 1935; Heptner, 1936; Dubrovskii, 1940; Heptner and Formozov, 1941; Vereshchagin, 1947, 1959; Kuznetsov, 1948, 1948a, 1952; Shereshevskii and Petryaev, 1949; Heptner, Turova and Tsalkin, 1950; Bazhanov, 1951, 1952; Korneev, 1952; Sludskii, 1953; Bannikov, 1954, Podkovyrkin, 1958; Afanas'ev, 1960; Sokur, 1960; Tembotov, 1960; Baziev, 1961; Stroganov, 1962 and other sources.

mouth of the Samarga. In this region, the range of the ermine extends along the main axis of the Sikhote-Alin' southwards approximately to 44°30′ (the latitude of the southern extremity of [Lake] Khanka). In the western half of the territory from the Amur to Sikhote-Alin', the boundary of the range apparently passes to the middle Bikin in the form of an arched line from the Khabarovsk region²¹.

Geographic Range outside the Soviet Union -

Occupies Europe from the shore of the Barents Sea southwards to the Pyrenees and Alps inclusive. It is distributed throughout Romania; in Yugoslavia it is only found in the north-southward to a line passing from the Danube at the junction of Bulgaria and Yugoslavia to the Istrian Peninsula (Riek—formerly Fiume). It is absent in Bulgaria, Albania, Greece and Turkey. To the west it occurs to Ireland and the Hebrides.

In Asia, outside the limits of the USSR, the distribution of the ermine is very poorly known. It occupies the extreme eastern montane regions of Afghanistan, Chitral, Kashmir and the region northeast of Peshawar (Hazara—the southernmost place of occurrence in Asia); it apparently lives in the Karakorum and in the western extremity of the Kunlun (the southwestern montane parts of Kashgariya); along the Tien Shan system it occurs eastwards at least to Hami. In the Mongolian Republic, the ermine is distributed everywhere, apparently, except flat semidesert and desert places; it is in the Gobi and Mongolian Altai, Khangai, Kentei and in the foothills of the Khingan. It is distributed in northeastern China (former Manchuria), and according to some data, "everywhere" (Baikov, 1915), but more accurate information is absent. Undoubtedly, it lives in Great Khingan and, probably, in the northern montane regions (Lesser Khingan, Il'Khuri-Alin'), and perhaps also in the east. Possibly it is found in North Korea. Its distribution in Japan includes at least Hokkaido and Honshu (Hondo).

The reference concerning its occurrence in Algeria (whence a separate form, M. e. algirica, was described) is, to a great degree,

²¹In Primor'e Territory, the ermine occupies the highest montane of Terneisk, Krasnoarmeisk, Tetyukhinsk, Kovalerovsk, Chuguevsk and Ol'ginsk regions. These, as well as data given above for Ussuri Territory, were communicated by Bel'skii (Vladivostok). According to Maak (1861), ermine occupies the Ussuri valley.

doubtful, especially if we take into consideration that in Europe, the ermine does not extend south of the Pyrenees and the Alps, *i.e.* that this form is isolated in its distribution. It is entirely probable that this name applies to the large southern weasel (M. n.*numidica), as it is considered by some authors (G. Allen, 1939).

In North America, the range occupies the entire Arctic archipelago, including Ellsmere Land (Grant), northern Greenland (northernmost point inhabited by the species) and eastern Greenland southwards a little to the south of 70°. The southern border of the range in the mainland, north of which ermine is encountered everywhere, forms a quite complicated line, in the west proceeding across middle California, approximately at 40° N. lat. including the northern half of Nevada, almost all of Utah, the greater part of Colorado (except the eastern) and northern New Mexico (the 673 southernmost point inhabited by the species is about 34° N. lat.). Thence, the border sharply rises to southwestern Alberta and southern Saskachewan, and then directs itself southeastwards to North Dakota and northern Iowa, then westwards across the southern ends of Lakes Michigan and Erie, to the Atlantic coast and Chesapeake Bay. It is met with in Newfoundland, on islands off the west coast of Canada, on Kodiak, on Unimak in the Aleutian group—(but not on the others) and, possibly, on several other islands in the Bering Sea which are located near the Alaskan coast (no indications for the Pribilovs) (V.H.).

Geographic Variation

In vast area of its range, the ermine reveals some geographic variation which, however, is not great. Its amplitude, in a morphological sense does not attain the dimension observed in the weasel, and is not more than that in other comparatively slightly variable species of the family and genus. It mainly bears a clinal character. The winter coat (its density, length), the color of the summer fur, and in part the general dimensions, are chiefly those that vary geographically.

Geographic variation of the ermine is still insufficiently studied, and representative of this, it is, apparently, exaggerated. Within the last decade, in reviews of our fauna, 10 subspecies were at first

^{*}In Russian original, erroneously as e-Sci. Ed.

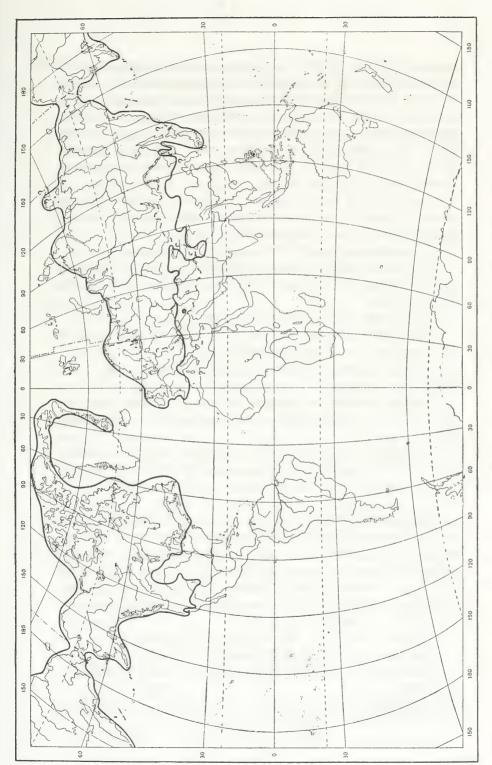


Fig. 245. Species range of the ermine, Mustela (Mustela) erminea L. V.G. Heptner.

accepted (Ognev, 1935); later, although with reservations—13 (Novikov, 1956). In recent times, a tendency to reduce the number of forms has been noted (Morozova-Turova, 1961). Apparently, the actual number of realistically characterized races is still less. Several foreign investigators accept many forms—21 for the Old World (Ellermann and Morrison-Scott, 1951) and 20 for America (Hall, 1945; Hall and Kelson, 1959), where the extent of the range is much smaller than in Eurasia.

The following forms may be provisionally accepted for our country (characteristics mainly after Morozova-Turova, 1961 and Stroganov, 1962, with modification).

1. Northern ermine, M. (M.) e. erminea Linnaeus, 1758.

Dimensions moderate or small. Facial part of skull is relatively short and broad. Condylobasal length of male skull 43–49 mm. On Kola Peninsula.

Outside the USSR-Scandinavian Peninsula.

Kola ermine are poorly known and the actual relationship of the name to this race requires confirmation.

2. Middle Russian ermine, M. (M.) e. aestiva Kerr, 1792. Dimensions moderate.

Color of summer fur—dark-tawny or chestnut. Individual variation in color is insignificant—from light-reddish to dark-tawny tones.

Body length of males (57), 215-M248.7-278 mm, of females (23) is 195-283 mm; tail length of males, 78-M92.4-105 mm, of females, 60-86 mm; length of hind feet of males 41.5-M46.2-55 mm.

Condylobasal length of skull of males (76), 41.0–M46.8–52 mm, of females (20), 39.8–M42.0–45.2 mm; zygomatic width of males, 21.5–M26.0–27.8 mm, of females, 21.2–M22.5–25.3 mm; interorbital width of males, 10.0–M12.0–13.0 mm, of females, M10.2 mm*; mastoid width of male skull, 19.0–M22.9–26.2 mm, of females, 18.0–M21.1–24.5 mm Zygomatic width constitutes 54.2–58.1% of condylobasal length.

European part of the USSR, except Kola Peninsula.

Outside the USSR, in Middle and West Europe.

3. Caucasian ermine, M. (M.) e. teberdina Kornejev, 1941 (syn. balcarica).

Dimensions small.

Color coffee- or reddish-tawny.

^{*}Only mean value in Russian original-Sci. Ed.

Body length of males 217 mm, of females, 175–190 mm; tail length of males, 84 mm, of females, 57–61 mm; length of hind foot of males 40 mm, of females, 27–30 mm.

Condylobasal length of male skull, 43.0 mm, of females, 37.8–39.3 mm; zygomatic width of males, 22.6 mm, of females, 20.0–20.6 mm; interorbital width of males 9.8 mm; of females, 18.4–18.6 mm. (Baziev, 1962).

Northern slope of middle part of Main Caucasus range (El'brus massif).

Outside the USSR-absent.

A very little known form, described as similar in dimensions and color to M. (M.) e. ferghanae (!). The independence of this form and its assigned characters require confirmation.

4. Tobolsk ermine, M. (M.) e. tobolica Ognev, 1922 (syn. ognevi, birulai, martinoi).

Dimensions large, on average somewhat larger than in the form aestiva.

Winter fur tall, dense and silky. Summer fur is also somewhat longer, denser and softer. Skull is large. Zygomatic width constitutes 54.6–M57.7–58.1% of the condylobasal length of its skull.

Body length of males (43), 200–M260–300 mm, of females, (35) is 200–M230–270 mm, tail length²² of males is 50–M90–120 mm, of females 50–M70–100 mm; length of hind foot of males 40–M45–48 mm, of females, 34–M37–42 mm; height of ear of males 18–M20–22 mm; of females, 14–M16–18 mm.

Condylobasal length of male skull (45), 43.4–M48.3–50.1 mm, of females, 39.6–M43.0–45.6 mm; zygomatic width of males, 24.8–M27.7–30.0 mm, of females, 21.4–M24.2–26.8 mm; interorbital width of males, 10.4**–M12.0–13.2 mm, of females 9.2–M10.8–12.0 mm, postorbital width of males, 9.6–M11.2–12.1 mm, of females, 8.2–M9.2–11.1 mm; mastoid width of males, 21.2–M23.6–25.2 mm, of females, 19.3–M21.0–22.2 mm.

In western Siberia, eastwards to the Yenisei and Altai, and in Kazakhstan.

Absent outside the USSR.

²²The minimum of this measurement (Stroganov, 1962) strongly differs from that given previously according to the same author (p. 668) and, apparently, here the mistake is self-inflicted*.

*In the Russian original, the word "Kroetsya" is used, which cannot be found. It may be a misspelling of "kropatsya", the reflexive form of the verb to bungle—Sci. Ed.

^{**}In Russian original, erroneously as 104-Sci. Ed.

For this form, in contrast to the form *aestiva* the following are considered characteristic: particularly large dimensions, widely diverging zygomatic arches and several other craniological features (Ognev, 1935; Morozova-Turova, 1961). According to Stroganov (1962), only characteristics of fur distinguish the Tobalsk ermine from the form *aestiva*.

5. Altai ermine, M. (M.) e. lymani Hollister, 1912.

Dimensions moderate.

Fur less dense than in *M. e. tobolica*. Color in summer fur with weakly developed reddish-brown tones, sometimes this tinge disappears completely. Skull similar to that of *M. e. aestiva*. Distance between zygomatic arches relatively narrow (zygomatic width constitutes on average about 55% of condylobasal length).

Body length of males (10), 218–M258–295 mm, of females, 185–M220–260 mm; tail length of males, 45–M75–105 mm, of females, 40–M60–90 mm; length of hind foot of males, 37–M44–48 mm, of females, 32–M36–42 mm.

Condylobasal length of male skull (14), 44.0–M48.4–49.4 mm, of females, 41.2–M43.7–45.2 mm; zygomatic width of males, 24.4–M27.3–28.7 mm, of females, 20.8–M24.4–26.2 mm; interorbital width of males, 11.8–M12.2–12.6 mm, of females, 9.9–M11.3–12.0 mm; postorbital width of males, 10.0–M11.4–12.8 mm, of females; 9.0–M10.2–11.7 mm; mastoid width of males, 21.3–M23.6–25.3 mm, of females, 19.2–M21.1–23.0 mm.

Weight of males (5), 145–M191–247 gm, of females (4), 106–149 gm (Altai preserve, winter; material from ZMMU).

Mountains of southern Siberia eastwards to Baikal (Altai, Sayan).

Outside the USSR—in contiguous parts of the Mongolian Republic. In the Gobi Altai and southern parts of Khangai and the Mongolian Altai, apparently, is another form.

6. East Siberian ermine, M. (M.) e. kaneii Baird, 1857 (syn. orientalis, naumovi, sibirica, kamtschatica, kanei, digna; sometimes the name arctica was, and still is applied, to this form).

Dimensions moderate, less than in M. e. tobolica.

Color of summer fur relatively light, with brownish-yellow tinges of various intensities. Zygomatic width constitutes about 56% on average of condylobasal length of skull.

Body length of males (22), 213-M260-325 mm, of females (7), 176-M212-222 mm; tail length of males, 70-M86-100 mm,

of females, 67-M72-77 mm; length of hind foot of males, 40-M43-48 mm; of females, 33-M38-43 mm; height of ear in males, 20-M21-22 mm, of females, 18-M19-20 mm.

Condylobasal length of male skull (24), 44.0–M46.0–49.2 mm, of females (23), 38.9–M40.9–44.3 mm; zygomatic width of males, 24.0–M26.2–28.8 mm, of females, 20.0–M22.3–25.2 mm; interorbital width of males, 10.1–M11.4–13.2 mm, of females, 8.8–M9.5–10.0 mm; postorbital width of males, 10.0–M11.0–12.5 mm, of females, 8.7–M9.7–10.9 mm; mastoid width of males, 20.1–M22.5–24.7 mm, of females, 18.0–M19.2–20.2 mm.

Weight of male (8), 102–M166–253 gm (Kamchatka, summer; material from ZMMU).

In eastern Siberia and the Far East including Kamchatka, except the Amur area and Ussuri territories, Trans-Baikaliya and Sayan.

Absent outside the USSR.

This form is not sharply distinguished, differing from western Siberian *tobolica* only in slightly lighter color and somewhat smaller dimensions. Differences can only be noted in series. The form is close to *M. e. arctica* from Alaska and may be identical with it.

7. Karagin ermine, M. (M.) e. karaginensis Jurgenson, 1936. Dimensions small, significantly less than preceding forms. Color of summer fur light-chestnut.

Body length of males, 220-230 mm; tail length 75-80 mm; length of hind foot 37-39 mm.

Condylobasal length of male skull, 40.5–M42.7–43.7 mm; zygomatic width, 21.6–M23.0–23.7 mm; interorbital width, 9.8–M10.1–11.0 mm; mastoid width, 19.3–M20.3–21.6 mm.

On Karagin Island along the eastern coast of Kamchatka. Absent outside the USSR.

This form is poorly known. Its independence must be confirmed in new material. It is possibly related to the form *kaneii*.

8. Trans-Baikal ermine, M. (M.) e. transbaikalica Ognev, 1928 (syn. baturini).

Dimensions relatively small.

Summer fur short and sparse, dark-brown in color. Skull small with relatively narrow interzygomatic area—zygomatic width constitutes on average 51.6% of condylobasal length of skull.

Body length of males (14), 225–242 mm, tail length 80–M85.7–90 mm, length of hind foot, 31–M40–45 mm.

Condylobasal length of male skull (94), 39.3–M43.6–46.1 mm, of females (26), 35.7–M38.2–41.7 mm; zygomatic width of males, 21.0–M23.2–24.5 mm, of females, 18.2–M19.5–23.7 mm; interorbital width of males, 9.1–M10.8–11.6 mm, of females, 7.9–M8.7–10.0 mm.

Postorbital width of males, 9.3–M11.0–12.0 mm, of females, 8.3–M10.1–10.7 mm; mastoid width of males, 19.1–M21.0–22.1 mm, of females, 16.8–M18.1–21.8 mm.

Weight of male (9), 101-M134-174 gm (Barguzin preserve, winter; material from Z[oological] M[useum of] M[oscow] U[niversity]).

In Trans-Baikaliya, Amur area, Ussuri Territory, Shantar Islands.

Outside the USSR probably in the eastern part of the Mongolian Republic and northeastern China (former Manchuria).

This form is close to the Altai, M. (M.) e. lymani and possibly both may comprise one form, which occupies all of southern montane Siberia and above-mentioned parts of the Far East. The name lymani has priority.

9. Fergana ermine, M. (M.) e. ferghanae Thomas, 1895 (syn. schnitnikovi).

Dimensions small.

Color of summer fur very light, straw-brownish or grayish, rarely with a film of red. The coat is short and soft. On the neck occur light spots, sometimes forming a collar. This is the lightest colored form of our fauna. Individual animals do not turn white in winter or become only partially lighter.

Body length of males, 205-M259-300 mm; tail length 70-M75-82 mm; length of hind foot, 40-M41-42 mm.

Condylobasal length of male skulls (9), 40–M43–45 mm; zygomatic width, 22.0–M23.3–25.5 mm; interorbital width, 9.5–M10.4–11.0 mm; mastoid width, 19.0–M20.6–22.0 mm.

Weight of males in summer (12), 121-M145-211 gm, of females (10), 60-M72.5-86 gm (material from Z[oological] M[useum of] M[oscow] U[niversity), from Tien Shan, mainly Zaillisk Alatau).

In montane Tien Shan and Pamir-Alaisk system.

Outside the USSR, parts of the range in Afghanistan and India and the westernmost parts of Tibet; found in adjacent parts of Tien Shan China.

It is a well differentiated form, to which the ermine of the Gobi Altai and adjacent parts of the Mongolian Republic (mongolica, Ognev) apparently belong.

* * *

The number of subspecies of ermine described from parts of the range lying outside the boundaries of the USSR, is great and evidently exaggerated, particularly for America. The following forms are usually mentioned: 1) M. (M.) e. hibernica. Thomas et Barrett-Hamilton, 1895—Ireland; 2) M. (M.) e. algirica Thomas, 1895-Algeria (see reference to this form in the section "Geographic distribution"); 3) M. (M.) e. stabilis Barrett-Hamilton, 1904—England; 4) M. (M.) e. ricinae Miller, 1907—islands of the Hebrides; 5) M. (M.) e. minima Cavazza, 1912—Switzerland; 6) M. (M.) e. nippon Cabrera, 1913-Japan; 7) M. (M.) e. mongolica Ogney, 1928—Gobi Altai (apparently, a synonym of ferghanae); 8) M. (M.) e. arctica Merriam, 1896—Alaska, northwestern parts of Canada, Arctic archipelago, except Baffin Land; 9) M. (M.) e. polaris Barrett-Hamilton, 1904—Greenland; 10) M. (M.) e. semplei Sutton et Hamilton, 1932—Baffin Land and adjacent part of mainland; 11) M. (M.) e. richardsonii Bonaparte, 1838-Newfoundland, Labrador and nearly all of Canada except the territories occupied by the forms named above; 12) M. (M.) e. cicognanii Bonaparte, 1838—region north and east of the Great Lakes; 13) M. (M.) e. bangsi Hall, 1944—region west of the Great Lakes; 14) M. (M.) e. murica Bangs, 1899—southwestern extremity of the range of the species in America (Nevada, Utah, Colorado and other states); 15) M. (M.) e. kadiacensis Merriam, 1896—Kodiak Island; 16) M. 677 (M.) e. anguinae Hall, 1932—Vancouver Island. From a small part of the range—the southern part of British Columbia, the state of Washington and western Oregon described forms are; 17). M. (M.) e. fallenda Hall, 1945; 18) M. (M.) e. invicta Hall, 1945; 19) M. (M.) e. gulosa Hall, 1945; 20) M. (M.) e. olympica Hall, 1945; 21) M. (M.) e. streatori Merriam, 1896; all have a limited or extremely limited distribution. Described from various islands of the Alexander archipelago and in part from the adjacent coastal mainland are; 22) M. (M.) e. alascensis Merriam, 1896; 23) M. (M.) e. initis Hall, 1944; 24) M. (M.) e. salva Hall, 1944; 25) M. (M.) e. celenda Hall, 1944; 26) M. (M.) e. seclusa Hall, 1944; 27) M. (M.) e. haidarum Preble, 1898 (V.H.).

Biology

Population. Ermine belongs among the number of abundant carnivores. Within the boundaries of its range, its numbers and density are, however, distributed very unevenly.

Indices of prepared skins, even those calculated per unit area (usually per 10 km²) by no means reflect the actual condition of the species population. They depend, to a very strong degree, on the extremely different intensiveness of harvest, the degree of control on animal stocks, and finally, on the condition of the population itself in the given trapping season. It is established that the catch and skin preparation increase with deficiency of ermine foods, but is not proportional to its numbers (S. Severtsov, 1941; Teplov, 1952). This takes place due to the greater ease with which hungry animals are caught in baited traps in a year following one with abundant reproduction.

The ermine is the most numerous in the forest-steppe regions of western Siberia and northern Kazakhstan. In second place follow the forest-steppe regions of Bashkir ASSR, Tatar ASSR and of the middle Volga region, and also the southern regions of Krasnoyarsk Territory, taiga and tundra regions of western Siberia and Komi ASSR. To the east, west, and south, the ermine is met with significantly more rarely. It is more frequent in the steppes of southern Ukrainian SSR and in the southeastern European part of the USSR (P.B. Yurgenson). Here, it is restricted almost exclusively to the deltas and floodlands of the great rivers.

For nine years (1924/25–1933), the average yield of skins per 10 km² was as follows: Bashkir ASSR—1.82, Siberia—1.07, Tatar ASSR—0.78, Ural—0.85, Severnyi Territory—0.60. In other parts of the range, abundance of ermine is considerably lower. Of course, these figures are connected not only with the abundance of ermine, but also with the development of the harvest in these years. At the present time, it has fallen significantly everywhere. At the same time, in a series of the main regions where the ermine was abundant, its numbers fell sharply, especially in the forest-steppe of western Siberia and northern Kazakhstan, due to the deterioration of food resources, destruction of shrubby growths along lakes, worsening of the hydrological regime, etc.

Habitat. Habitats of the ermine are sufficiently variable. Nevertheless, in different geographic zones, it is closely associated with near-water biotopes.

In the tundra zone, the ermine prefers the banks of rivers, riparian meadows and thickets of bushes. It also lives along the slopes of valleys and in rocky places. The latter are particularly typical for montane tundra. It also willingly holds to the fringe of the forest-tundra. In the forest zone, it prefers most of all the whole of the banks and floodlands of rivers and creeks, the shores of forest lakes, floodlands and marshy sedge meadows with shrubby thickets and hummocks, etc. Forest massifs are untypical habitat for the ermine, although here it is met with almost everywhere, but not often. In forests, old cluttered burned areas and glades, the edges of forests and shrubby areas (especially those near settlements and arable lands), but deep within forest massifs it prefers cultivated fir and alder as well as the forest meadows and old hay-stacks. It does not avoid settlements and gardens near them. In winter, it often searches for food in grain stores and heaps of straw.

Reduction in area of cut-over areas and burns resulting in age changes in the cover of forest vegetation covering them, leads to a sharp decrease in the number of ermine in the forest and to decrease in the area inhabited by it (for instance, 100 times). As a result of this process, the greatest density of ermine occupation in fir forests is found in the cultivated fir plantations which are teeming with life. These are original surviving stands, whence under favorable conditions ermine spread out into other stands. Flooded fir-groves when they cover the whole forest massifs, favor anew the settlement of animals in newly-appearing clearings and burns from many points (Yurgenson, 1959).

In the forest-steppes and steppes, ermine clearly avoid open expanses of steppe and restrict themselves to floodland meadows with osier thickets along the valleys of rivers, along steppe clearings and their edges, in birch-groves along swamps, in hummocky swamps and in weedy thickets around steppe lakes. It is also encountered along steppe ravines and gorges. It often appears in dwellings not only of small settlements, but also the outskirts of cities.

In the Altai mountains, ermine occupies rock slides with pika colonies, and dry alpine meadows inhabited by the narrow-skulled vole [Microtus gregalis]. Here, it more willingly lives in places with shallow snow cover. In selecting stands, the ermine is more plastic than sable and Siberian weasel. It is more rarely met with in dark coniferous taiga than in thin, sunlit stands. On coastal

cliffs it lives in rock slides, and catches water voles by unfrozen springs; in montane taiga, it is an inhabitant of rocky sections and open *elans**. In winter on montane balds and bushy tundra; it sticks to stands with willow ptarmigan and lives for a long time in rock slides inhabited by pikas (Dul'keit, 1956). In the mountains of southern and southeastern Kazakhstan places of its occupation include shrubby thickets, apple, juniper and fir forests and highland fescue steppes (Sludskii, 1953). The ermine everywhere prefers floodlands to other types and without them, it spends much of its time near water. In Tatariya, in flooded areas, the density of ermine is six times higher than in plakorn* dry regions (Aspisov and Popov, 1940).

Food. According to feeding type, the ermine belongs among animals with a limited assortment of food. In its food mouse-like rodents (in the broad sense) predominate, but in contrast to the weasel which almost exclusively feeds on small voles, a considerable place in its food is occupied by the larger rodent species—water vole, common hamster, pikas and others, which the ermine overpowers in their burrows and which the weasel cannot master or with great difficulty.

More or less constant, but of secondary significance, are small birds, and sometimes fish and shrews. More rarely there are amphibians, reptiles (lizards), and insects. All of these secondary and rare foods in the diet of the ermine, and also berries in Lapland (Nasimovich, 1949), are a sign of food deficiency, deprivation, and simply starvation. In the Ob' preserve, 156 cases of bird nests destroyed by ermine were recorded during four years. Of these in 60 cases it was nests of the pied flycatcher, in 59—starlings, in 16—great tit, in 8—spotted flycatcher, in 6—wryneck, and in 4—white wagtail (Karpovich and Sapetina, 1958). In years with high and prolonged flooding, the number of cases grows since bird nests are destroyed on the ridges and islands during inundation. Here, nest destruction comprises 14%, while outside the flood zone 0.5%.

In the ermine of floodlands and banks of watercourses, besides the water vole and gray vole [Clethrionomys rufocanus], the root, common and field voles [Microtus oeconomus, M. arvalis, M. 680 agrestis] predominate; in forest areas, various species of red-backed voles; in tundras, lemmings also. Ermine rarely attack the commercial

^{*}Local word?-Sci. Ed.

Table 63. Geographical characteristics of ermine nutrition (in % of total number of data)

¹Famine year.
²Squirrels decrease.

animals and birds—even more rarely with success. However, cases of ermine feeding on muskrats, probably young, have been recorded.

Geographic variation in nutrition of ermine is not great. Variations in the predominant food composition in different years are significant. They depend on the numerical composition (yield) of the different species of mouse-like rodents. These variations are partially presented in Table 63 (data from Komi ASSR, Pechora and Kirov district), and for Pechora-Ilych preserve over 12 years—in Table 64.

In Laplandia, in years with abundant voles and lemmings, an ermine caught four animals in one hunt (Nasimovich, 1948). It eats no more than two and in a famine year, one satisfies it. With an abundance of prey, it consumes only the brain or leaves it untouched on the trail, killing significantly more animals than it is able to eat. The daily food norm is about 50 gm, *i.e.* about 25% of the live weight of the animal. The ermine usually makes a stockpile of food. Found among its "stores" were up to 5 common hamsters, 5–8 water voles, up to 10 small mouse-like rodents and 4 shrews at one time, etc. (Zverev, 1931 and others).

Home range. With the formation of snow cover deeper than 12-15 cm or more, each ermine occupies a defined home range.

680 Table 64. Nutrition of ermine in the winter period in Pechora-Ilych preserve over a 12-year period (% of occurrence)

Type of food	Range of fluctuation in occurrence	Average for 1938/39 to 1950/51
Voles	0—72.7	47.9
Shrews	5.9—66.9	24.2
Tetraonid birds	0-13.3	7.8
Other birds	0-35.8	11.8
Squirrel	0-11.2	1.9
White hare	0-7.4	0.7
Carrion	0-6.7	1.5
Insects	0-7.1	0.5
Percentage of empty stomach	s 29—58	46.8
Average weight of stomach contents	0.5—3.0g	1.35g

Note. From data of the "Nature Chronicle" of Pechora-Ilych preserve.

This area is divided into a series of ranges of daily activity, with repeated visits each 3–10 days (Zharkov, 1941). Such ranges of mingled living animals often overlap each other.

In sparsely treed, northern montane Murmansk district, the area of the home range varies within limits of 50-90-100 hectares (Nasimovich, 1948). In the forested regions of the middle belt, its dimensions shift from 10-15 to 100-200 hectares, depending on food. Here, the range of daily activity at the start of winter equals 5-6 hectares each, but by the end it reaches 100-200 hectares (Shibanov, 1935). In the floodlands of Tatariya, the area of the daily activity range varies from 7.7-8.8 up to 31.5 hectares. The area of the daily activity range of males is considerably greater than in females: in males 15-20 hectares, average 29.5;* in females up to 8 hectares, average 7.1 hectares. Sometimes, a group of ranges are observed, inhabited by 5-12 individuals and alternating with ranges of lower density of occupation. It is possible that these are mingled ranges of the dispersing litter (Zharkov, 1941).

Burrows and shelters. The ermine does not dig a burrow independently. It often uses the burrows and nest chambers of the rodents it kills—water voles, hamsters, Siberian chipmunks, and others—for the litter young, and even more often as a temporary shelter. The nest chambers in the brood burrows are lined with the skins and underfur of mouse-like rodents, rarely only with dry grass. Sometimes, the brood shelters are located in very unexpected and seemingly unsuitable places, for example among logs piled against the wall of a house in a large village (Kazakhstan; V.G. Heptner) and without any kind of lining at all.

The ermine also lives in old and rotting stumps, under tree roots, in heaps of brushwood, haystacks in floodland meadows, in heaps of straw, in old haystacks, in bog hummocks, in the cracks of vacant mud buildings, in rock piles, rock clefts, and even in magpie nests. It also occupies the hollows of trees; it particularly often uses these during periods of flooding. Males and females live separately, but near each other (Velizhanin, 1931; Zverev, 1931; Yurgenson, 1932; Nasimovich, 1948; Sludskii, 1953).

The ermine has no permanent shelters in winter, and uses the opportunistic ones near its hunting places. It rarely returns to its old place of day rest. Such shelters occur under rocks, in the roots

^{*}There is an obvious misprint here, but what the correct values are could not be determined—Sci. Ed.

of trees, under logs covered with snow, etc. However, in Yakutiya, apparently, it uses one burrow throughout the entire winter (Belyk, 1958).

Daily activity and behavior. The ermine is mostly active in the twilight and night hours of the diel period, but sometimes it comes to pass that it is encountered during the day. The light regime in high latitudes substantially influences the diel cycle of the ermine. In the period of the polar day, about 70% of the occurrences of this animal take place in the night hours (1800-2400). In autumn (September-October), when the night is becoming darker, it often is encountered during the day. In the first, darkest half, of winter (15 Nov.-1 Feb), the ermine most often hunt in the morning and during the day (morning-11 encounters, day-7, evening and night-5: Nasimovich, 1948).

During periods of severe frosts activity of the ermine notably decreases. With its available stores of food it can remain, in this event, for 1-2 days, as well as after a snowfall. During snowstorms it is active (Velizhanin, 1951; Zverev, 1931; Zharkov, 1941; Nasimovich, 1948). In winter, it goes out for prey 1-2 times per day.

In winter, during one excursion, the ermine travels 0.5–8.0 km (about 3 km on average). In short lateral loops its wandering "shuttle" route constitutes 1/3 to 2/3 of its daily journey (Nasimovich, 1948).

The ermine swims and climbs well, but it is fundamentally a terrestrial animal. It can move freely in the underground passages of rodents—water voles, hamsters and pikas, but it is not able to penetrate the burrows of small voles. The ermine is very bold, brave and cunning. The prey is killed in the same manner as the weasel, by biting the skull in the occipital region. In a situation, where it is cornered, it dares to attack humans. In the tents of peoples of the far north it often makes itself an intrusive lodger, plundering stock of meat, fish and other products.

The movement of the ermine is quick and dexterous, but somewhat fidgety. It is extremely curious, a property which is closely connected with careful examination of the hunting range when acquiring food.

Seasonal migrations and transgressions. Sedentariness within the range boundaries is typical for ermine in winter in years when it is sufficiently supplied with food; when unbalanced by

starvation or insufficient food, then it is obliged to roam widely. In Lapland preserve, an ermine roamed an area of 25 km² (Nasimovich, 1948).

Sometimes, the abundance of water voles or mouse-like rodents and characteristics of their distribution within an area lead to massive displacement of ermines for considerable distances. Such migrations were noted in western Siberia in 1928 and were compared with mass reproduction of water voles in the northern regions (Zverev, 1931). The mechanism of such migrations remains almost unexplained.

In a series of localities, moreover, local migrations are observed of seasonal character. Thus, in Voronezh forest-steppes, ermine in winter move down from highland oak groves to floodland black alder forests—levadas* (Severtsov, 1850)** and in springback. In forests of the middle belt, some ermine move from the edges of the forests and shrubby thickets to populated areas—grain stores, straw piles and haystacks, feeding on voles and mice concentrated there. In the floodlands of large rivers, during the time of spring flooding, ermine are concentrated in the inundated ridges where an abundance of food in the form of mouse-like rodents migrating thence from the floodlands are found (Aspisov and Popov. 1940; Zharkov, 1941 and others). In Oka preserve, during time of the spring flood, on unsubmerged islands, five pairs of ermines were found in an area of 36 hectares, which constitutes a density of 278.0 per 10 km² (Karpovich and Sapetina, 1958). In the Lapland preserve, in connection with dispersal of forest voles, local migrations from the pine woods and burns to the fir groves for a distance of 10 to 15 km were observed (Nasimovich, 1948).

Reproduction. Reproduction of the ermine is still entirely insufficiently studied. It has one sexual cycle per year. Spermatogenesis in males lasts for five months of the year, and sexual activity for four months (middle of February-first half of June for northern Kazakhstan). In the nonfertilized females, ovulation is periodically repeated monthly. They are capable of being fertilized throughout the whole period of male sexual activity. In adult females, fertilization for the most part takes place just after parturition. Young females are fertilized in summer. During the course of pregnancy, there is a prolonged latent period, probably with

^{*} Local name?-Sci. Ed.

^{**} Misspelled Severtsev in Russian original? Not in Lit. Cit.—Sci. Ed.

variable duration. After it, the active development of the embryos lasts not more than one month.

The number of young in a litter varies from 2–18, more often 4–8; for northern Kazakhstan, the average number of young is 8.7 (Tikhvinskii, 1937; Grigor'ev, 1933; Lavrov, 1944). In Yakutiya, estrus usually occurs in April–May, but sometimes even in the first half of April, embryos are observed easily by eye. Their number ranges from 7–8 up to 12. In Yakutiya, the number of males in a litter is greater than that of females (Belyk, 1958). In populations of West Siberia, males constitute 53% and females—47% (Zverev, 1931). In northern Kazakhstan, males are 61–65% of the population; on average, there is one female for 1.75 males (Lavrov, 1944). The sex ratio changes by season, reflecting the degree of activity of the different sexes; sex ratio also changes substantially by year, depending on environment conditions of the external environment. In unfavorable years with insufficient food supply, the number of females increases (Lavrov, 1944).

In ermine of Yamal, two peaks of reproduction are observed: in late winter and in summer. In July-August, the main mass of the current year's females participate in the rut, having attained sexual maturity at the age of 3-4 months. Adult males also take part in it (these born in the preceding year), because the males of the current year attain sexual maturity only in the following year.

After pregnancy which lasts (with the latent period) 9–10 months, the young are born in April–May. At that time, those females who have not, for various reasons, participated in the summer rut, come into heat: in them pregnancy is only six weeks, the young also appearing in May–June (Kopein, 1961).

The timing of sexual activity and reproduction is subject to geographic variation, but this question has not been studied.

Growth, development and molt. The young are born in March-April, blind, naked and helpless. Both parents participate in their care (Bekshtrem, 1931; Sludskii, 1953 and others). When rivers overflow onto floodlands, they transfer their young to a safe place. At the age of one month, the still-blind young are already covered with relatively dense fur and have well-developed canines and molars. At the age of 2–3 months, the young attain the size of the mother, differing only in fur quality (Lavrov, 1944). At the end of June–July the young are independently capturing food, but the brood still has not dispersed (Zverev, 1931). Young males attain

683

adult dimensions only in the second year of life. Young females become sexually mature very early—at an age of 2–3 months and, probably, are quickly made fecund. Spermatogenesis is not yet observed in young males in their first year of life (Lavrov, 1944).

Two molts occur in ermine: spring and autumn.

Enemies, diseases, parasites, mortality, and competitors. Red fox, golden eagle (Nasimovich, 1948) and sable (Baturin, 1923; Dul'keit, 1929; P.B. Yurgenson) are among the immediate enemies of the ermine. References to other animals are based on general considerations, not confirmed facts.

In the Sayan mountains, the ermine as well as the Siberian weasel occupy successional habitats which are sometimes isolated from the habitats of sable, and the latter animal occupies the widely distributed primary habitats. The ermine coexists better with sable than does the Siberian weasel. Dispersal of ermine takes place at the end of November-beginning of December when the sable has already determined its habitats. Concentrations of ermine tracks are observed in places sable and also squirrel have left: floodlands of rivers, burns, and places of heavy snow accumulation (Dul'keit, 1959).

Diseases of the ermine are insufficiently studied. The ermine is weakly susceptible to tularemia (Lavrov, 1944); disease of a tubercular character and a type of infectious encephalitis type have been noted (Yurgenson, 1931; Lavrov, 1944). Infestation by tapeworms is not great—38.5% (Lavrov, 1944). The helminth fauna of the ermine is not rich (10 species), and the degree of infestation is usually insignificant. Only skryabingulosis is of substantial pathological significance. In different years, the degree of infestation reaches 50% of the population, and the number of individual worms in one ermine—up to 45. Beside mortality, skryabingulosis causes a reduction in fertility. Tapeworm invasion of the ermine is particularly dangerous in poor food years (V. Popov, 1943, 1947; Lavrov, 1944).

The extent of longevity in the ermine is unknown.

Age determination beyond 2 years by the tooth wear method (Stroganov, 1937) is not confirmed by accurate data and therefore it is not insufficiently founded. In populations of the species, animals up to one year of age constitute, according to commercial capture data, from 38.5 to 69% (average 54.2%), those 2 years old—from 20.8 to 33.8% (average 24.5%) and those above 2

years—from 9.7 to 37.4% (average 21.3%). In evaluating these figures, selectivity of the harvest must be taken into consideration. In Tatariya, the quantity of juvenile animals varied over 11 years from 19.3 to 63.9%, constituting an average of 50.8% (V. Popov, 1947). In Yamal, among the ermine inhabiting the tundra in summer, juveniles constituted 72.5% of the population as a whole, but adult, the reproducing part of the population, constituted 27.5%. In winter, young ermine constituted 94.4% of the population, and adults—5.6% (2,373 specimens). These data speak to the higher mortality among adults. Usually, mortality of young is higher.

For ermine in the far north it has been shown that average length of life is 1 year, and the period of complete turnover of the population—3 years. Death of adult ermine occurs in autumn, and juvenile females play the main role in increase in the number of ermine in the following year (Kopein, 1961). The argument for increased autumn mortality of adult ermine is not ecologically based; since in autumn, the number of mouse-like rodents—the main food of ermine—is highest.

In Murmansk district, the principal reason for ermine mortality is starvation (Nasimovich, 1949). In Kazakhstan, ermines die in great numbers during the time of great steppe fires; in connection with drying up of water bodies in the steppe; during flooding of the steppe from snowmelt water in spring; from hunger as a result of frozen ground; and from killing off of steppe rodents as a result of tularemia and other epizootics (Sludskii, 1953).

In years of food shortage, the emaciated animals undoubtedly die also during flareups of [disease] invasion and epizootics. In Kolyma territory, death of young ermine occurs during a cold spring, with abundant precipitation and high water in rivers (Belyk, 1958). The same is observed in the Volga area (V.I. Tikhvinskii).

Harvesting has been shown as a very powerful effect on the process of mortality in populations. Its influence is selective: the young, less cautious animals are caught in the first series, and then males—more often than females.

The results of selective harvest are determined by winter food conditions. With abundant food, ermine are numerous, but rarely enter traps, and on the contrary, they go into traps well and are caught in years of starvation with little food. Hence, the increase in prepared skins is in the season following a maximum rise in the number of ermine, when there is insufficient food for the

reproducing animals. This usually occurs with depression in number of mouse-like rodents (Severtsov, 1941; Teplov, 1952).

All carnivorous animals and birds which mainly feed on mouse-like rodents may be competitors of the ermine.

Population dynamics. The ermine population is subjected to considerable changes. Within the boundaries of the range, these changes do not proceed equally and simultaneously everywhere, but all the same are covering a considerable extent. Within their borders, subsequent changes in ermine populations are determined by one and the same similarly directed changes in conditions of the external environment.

In the process of these changes, numbers of ermine may change within different limits: in Murmansk district, up to 30-fold (Nasimovich, 1948), in the Tatar ASSR 54-fold (Aspisov and Popov, 1939), and in the southwestern part of Kalinin district (20 years of observation) by more than 189-fold (Yurgenson, 1959). In the first 8 years of observation, fluctuations here were only 2–6-fold; in the post-war years, the population decreased very sharply, as was also observed in other districts of the USSR. In northern Kazakhstan, fluctuations in prepared skins was 3–7 times, and the catch of individual hunters fluctuated from 2–3 up to 100 individuals; *i.e.* within 30–50 times (Sludskii, 1953).

Beside the comparatively short-term fluctuations with a time interval of 3–4 years between two peaks in ermine numbers in Murmansk district, 5–6 years in the southwestern part of Kalinin district and in the upper Pechora—6 years etc., there are, apparently, more prolonged fluctuations within which short-term fluctuations are embedded. Concerning these prolonged fluctuations data are still insufficient. In northern Kazakhstan, periods of depression in numbers last for 5–6 years, and the periods of growth are up to 3–4 years (Sludskii, 1953).

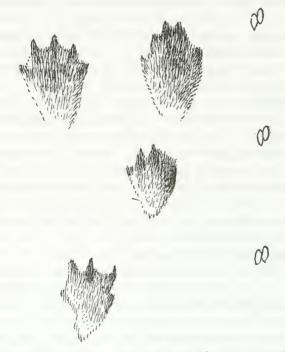
685

The ermine population changes in the course of a year. The greatest number of animals is reached in spring and the beginning of summer, and the least by the end of the harvest season. How great is the significance of the harvest is obvious from the fact that in the floodland of the Kama, the density of ermine at the beginning of the harvest was 52.0 per 10 km², and by its end—only 18.5 (Zharkov, 1941).

The reasons for the changes in numbers may be:

1) changes in availability of its main foods (voles, water voles); 2) helminth invasion (chiefly in the form of skryabingulosis) and insufficiently exposed epizootics; 3) fluctuations in levels of spring flooding in inundated sections, which with high levels causes the death of litters. The significance of flooding is thus of two kinds: moderate floods are favorable, causing a considerable concentration of mouse-like rodents in unsubmerged parts in the period when young are being fed, but deep flooding is fatal; 4) steppe fires, extensive frozen ground, drying out of steppe water bodies and spring flooding of the steppe by snow-melts cold rains etc.

Field characteristics. In the snowless period of the year, the ermine, its tracks or excrement are not easily detected. In the period of snow cover, traces of ermine activity are easily discovered on the snow surface. The ermine moves almost exclusively in jumps, leaving on the snow paired, sometimes, somewhat obliquely situated, footprints. Tracks and jumps of the males are always larger than those of females, but the tracks of young males may be confused with those of adult females.



685 Fig. 246. Tracks of large ermine on loose snow lying on a crusted surface. Gait unhurried—the prints are situated as a quartet. On the right, the scheme of ordinary jumps with paired tracks. Neighborhood of Gorkii. 30 December 1916. Sketch by A.N. Formozov, about 2/3 of nat. size.

The tracks of ermine differ from those of weasel by their larger size, a much larger search route and by the fact that ermines, when walking, sometimes "trots"; *i.e.* leaves a triple print track as in hare or squirrel, which is not observed in weasel. The ermine digs under the snow significantly more rarely than the weasel, and exits onto the surface after 1–1.5 m.

The length of jump of the ermine on the snow varies from 30–40 to 82–100 cm; in weasels their length is 25–36 cm, maximally–45 cm. On packed snow, ermine are able to make jumps up to 1.5 m and more (Formozov, 1952). The average length of prints of the male track is 62 mm, of female—46 mm (Nasimovich, 1948). The length of jump of the Altai ermine is equal to 25–50 mm; it sinks into the snow 2–5 cm, and its weight load on 1 cm³ of track is 10 gm (that of sable and Siberian weasel is 12–14 gm, of weasel—7–8 gm) (Dul'keit, 1956).

Excrement of ermine takes the form of a spirally-rolled plait thinned at both ends, and consists of underfur and bone fragments. Its thickness is usually about 0.5 cm, and length is not more than 10 cm (P.Yu.).

Practical Significance

686 The ermine is one of the fundamental items of mass commercial hunting of our country. Its catch in the USSR constitutes not less than half of the world catch. Beside this, our country offers ermine skins of the highest grade to the world fur market (Berezovskii, Ishimskii and other standard fur types). The best grade of the North American ermine may only be compared with the 9th grade in quality type of our standard.

Ermine fur is exclusively used for decoration. Because of this, its demand and price depend, to a great degree, on style and is distinguished by its significant instability.

Regions where ermine harvest has grown up as a specialty are relatively few. It is significantly more often trapped incidentally, or near the vicinity of villages. Therefore, the ermine is, on the whole, exploited around our country insufficiently and unequally.

All methods for capturing ermine may be divided into two groups: hunting with dogs, with or without guns; and capturing ermine with box-traps and jaw-traps. Hunting with guns cannot be recommended because of damage caused to the skin by shot,

staining the flesh side of the skin with blood, and almost unavoidably dirtying its fur, which lowers the price and quality; blood-staining is also unavoidable when an ermine is caught and throttled by a dog.

Of the passive means of snaring, metal-arch snap-traps, dead-fall box traps, kulemka*, and box traps actuated by strong elastic—cherkan*—are successfully employed. Less widely distributed are various nooses (most often, of hair) which are sometimes mounted on a frame or crosspiece (called a "little stool"). All these traps are used as "entrance-gates", on tracks or at holes and with bait (P.Yu.).

SOLONGOI²³

Mustela (Mustela) altaica Pallas, 1811

- 1811. *Mustela altaica*. Pallas. Zoographia Rosso-Asiatica, 3, p. 98.; Altai.
- 1823. *Putorius alpinus* Gebler. Mémoires Soc. Imp. Natur. Moscou, 6, p. 212. Ridder mines, Altai.
- 1857. Mustela temon. Hodgson. J. Asiat. Soc. Bengal, 26, p. 207. Sikkim, Himalayas.
- 1870. Putorius astutus. Milne-Edwards. Nouv. Arch. Mus. Hist. Nat. Paris, 7, Bull., p. 72. Mupin in Sichuan, China.
- 1911. Mustela longstaffi. Wroughton. J. Bombay Nat. Hist. Soc., 20, p. 931. Teza, upper Sutlej valley, Himalayas.
- 1914. Mustela sacana. Thomas. Ann. Mag. Nat. Hist., 13, p. 566. Vic. of Przheval'sk, Tien Shan.
- 1928. Kolonocus alpinus raddei. Ognev. Memuary Zool. otdeleniya Obshch. lyubit-estestvozn., antrop. i etnogr., 2, p. 9. Kulusutaev post near Zun-Torei Lake (Tarei-nor), southeastern Transbaikaliya.
- 1928. Kolonocus alpinus birulai. Ognev. Ibidem, p. 10. Lyangar in West Pamir (northern part of Darvazsk range, Obikhangou river) (V.H.).

*Local names of traps—Sci. Ed.

²³The name is derived from the Mongolian *solongo*, and is current in Transbaikal. In some places, the animal is also known as "*suslennik*" and "mountain polecat". In the fur trade, the name "mountain *kolonok*" is employed.

Diagnosis

Color from bright ocher-reddish to straw-ocher or from nut-brownish to brown. Lighter below than above, transition from dorsal color to ventral color lower part gradual or border sharp. Tail monotone, without black terminal half. Dark coffee-brown field ("mask") on head absent. White field with blurred border on upper and lower lips and chin. Skull relatively elongated (mastoid width usually less than half condylobasal length of skull); postorbital constriction with abrupt isthmus almost immediately behind supraorbital processes, its lateral outlines not parallel. Dimensions relatively small—condylobasal length of male skull less than 55 mm, of female, less than 48 mm (V.H.).

Description

In general appearance, dimensions and habits, the solongoi is very similar to ermine, but differs in its somewhat larger head, longer and fluffier fur, the more furry tail. Tail length more than 1/3 body length—with terminal hairs, about 1/2. Claws white.

Winter fur dense, and although short (length of guard hairs on sacrum 12–18 mm—only slightly more than ermine), quite luxuriant. Tail covered by hairs of equal length and equal thickness over its whole length as in ermine, but somewhat more luxuriant. In some forms, tail hairs very strongly lengthened, even more luxuriant. Soles of feet completely covered with hairs; digital and sole pads not visible.

In winter fur (Altai), general color tone of upper side of body pale straw-ocherous or clay-ocherous; guard hairs are shiny, with brown tips. In middle of back, color more intense. Upper part of head is somewhat darker and duller than back (here yellow tone of underfur drops out), but "little cap" very weakly defined in form of darkish overlay, sometimes not developed at all. Dorsal color of sides gradually passes into considerably lighter straw-ocherous with yellowish-red tones or to whitish-ocherous color of venter, chest and throat. Chin, most anterior part of lower surface of neck, lower and upper lips whitish or white or almost white. White color of lower neck surface imperceptibly passes into color of lower part of body. Concerning white areas on upper lips, the same applies, but these areas are usually quite sharply demarcated from color of

upper head. On throat, chest, and base of paws, vague whitish spots sometimes occur.

On neck, dorsal, as well as lateral color gradually passes into ventral color; on head, borders of colored areas quite sharp due to described light fields. Small dark spot on light background usually found behind corner of mouth. Tail same color as back, with reddish tint, similarly colored above and below, *i.e.* darker than venter. Upper parts of legs same color as back, and lower parts—as sides, inner parts colored like venter. Feet dorsally lighter than back—straw-colored or whitish. Covered ventrally by dense whitish-silvery hairs which conceal callosities.

Summer fur (Altai) considerably shorter, coarser and more sparser than winter fur. Hairs on tail considerably shorter and sparser, causing it to appear thinner. Lower surface of paws more weakly furred, digital and sole pads quite noticeable.

Color of summer fur very sharply different from that of winter and much darker than it. Upper side of body dark brownish-ocherous color, more intense in middle of back. Sometimes color of spine weakly delineated against general background of back. Dark area of middle back extends along upper neck and covers top of head. Sometimes top of head somewhat darker than middle back, and darker "cap" without sharp outlines marks itself on head. Sides somewhat lighter than back—nut-brown. Lower body light-ocherous, even whitish-ocherous, throat slightly brighter. Border between color of lower body and the sides completely sharp, almost as in summer ermine, but situated much lower.

Lower surface of paws dark, like back, upper has color of sides, fur on digits whitish above. Sometimes, small (about 1 cm in diameter) dark spots of same color as sides occur on lower surface of body. Region between rami of lower jaw lighter than general color of lower body, sometimes whitish or almost white. Upper and lower lips white or whitish. This color on lower jaw imperceptibly passes into color of chin, throat and neck. On upper lips, a narrow white field usually quite sharply demarcated from dark color of head. Sometimes, white color of upper lips poorly developed—narrow or weakly lightened and gradually merges with dorsal color. Behind corner of mouth, a bit below border between top and bottom, a small chestnut dot occurs.

Individual variation in color is usually of a fluctuating type and of small amplitude. Sexual dimorphism in color is absent.

1033

Young up to two months are covered by a short, fluffy, dull, dark fur. In the first winter, they are clothed with adult pelage. Geographic variation in color is quite significant and is expressed in general tone of winter and summer fur—either lighter or darker depending on brightness, degree of contrast between winter and summer fur, sharpness of border between dorsal and ventral color, and in presence or absence of border itself (gradual transition)²⁴, intensity of ventral color, which may be almost white and other characters. Essentially, this variability, in this way, bears not only a quantitative but also a qualitative character.

The skull of the solongoi is, in some respects, similar to that of the Siberian weasel [M. sibirica], but differs from it in a series of essential characters. It is not so narrow, long and elongated, having a shorter, wider and more swollen braincase. The region of the postorbital constriction is relatively short with a well defined isthmus, located near the supraorbital processes. The narrowest part of the postorbital region ("isthmus") lies on the line connecting the supraorbital processes, at a distance less than half the distance between the ends of these processes. The lateral outlines of the postorbital region of the skull (region of the frontal bones) are not parallel (or more or less parallel), but form angles, the apices of which are directed towards each other (toward the sagittal plane of the skull).

Infraorbital foramina small, oval, their longitudinal diameter less than or equal to longitudinal diameter of upper canine alveolus. Interpterygoid area usually narrows forwards, and its general outline has an angular form, apex directed forwards. Auditory bullae are elongated, in plan a smooth rectangular form,

²⁴This distinction between the color of the summer and winter fur is neither noted nor emphasized in our literature, first of all; and then, that in the summer solongoi there may be such an "erminish", bicolored type. Usually, even in the time of Satunin and to this day guides and monographs published in 1962 and 1965 (edited by I.I. Sokolov, A.N. Formozov and A.P. Kuzyakin) have on the contrary underlined, contrary to other groups of the genus, that in opposition to other groups of the genus "color of the dorsal and ventral sides ... is monotone-yellowish-red" or "the color ... on the back and on the belly is the same", "color of the back and abdomen is identical... "color of dorsal and ventral sides of the body is red, dark-yellow or grayish yellow" etc., and that the solongoi is completely identical to the Siberian weasel in color. Because of this, color is considered one of the main characters for the group "Kolonocus" and is considered as such in keys, diagnosis etc. So categorical a formula not only presents an incorrect representation of the species characteristics, its systematic position and geographic variation, but also makes difficult the simple identification of the solongoi in several regions.

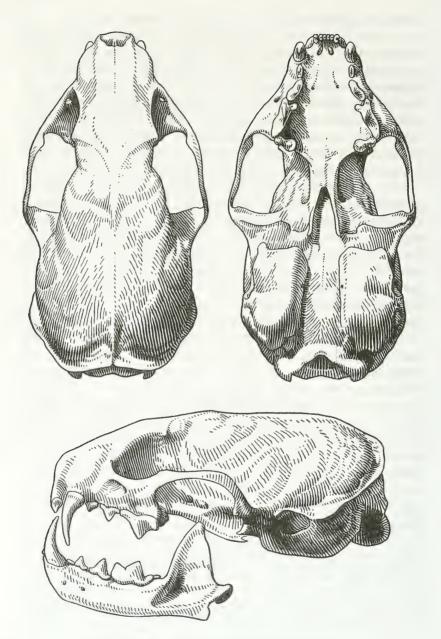


Fig. 247. Skull of solongoi Mustela (Mustela) altaica Pall.

with inner borders of almost parallel lines. Width of auditory bullae approximately equal to half its length. Distance between bullae usually greater than width of the hard palate at anterior part of interpterygoid depression. Zygomatic width approximately corresponds to width of skull in mastoid region. Zygomatic arches weak. Protuberances, crests, etc. unnoticeable; sagittal crest weakly defined, occipital crest somewhat larger. Frontal area elevated, profile of facial region slopes down from it quite suddenly. Teeth relatively strong.

On the whole, the solongoi skull by comparison with the Siberian weasel skull with which it is usually affiliated, has several infantile features. As regards degree of its development, it may be equated with the ermine skull.

Age and sexual differences in the solongoi skull have not been specially described. In general, they correspond to those mentioned above for ermine. The female skull is considerably smaller and somewhat lighter than the male skull, with less defined protuberances, crests, etc. Skulls of young animals have more brain case, which is well marked in animals up to one year old, but in the second winter of life, the skull acquires all the features of the adult animal. Individual variability in the skull is great, but does not exceed that in other species. Geographic variation of the skull, at least within the boundaries of the USSR, is neither developed nor noticeable, with the exception of one race.

Structure of the os penis is typical for the majority of the species of this genus, *i.e.* distal end forms an upwardly bent hook.

Dimensions of the solongoi are close to those of ermine. Body length of males is 224–287 mm, of females, 217–249 mm; tail length of males is 108–145 mm, of females, 90–117 mm; length of hind foot in males is 39–47 mm, of females, 33–45 mm; height of ear in males is 16–21.6 mm, of females, 14.0–20.2 mm (Sludskii, 1953; Stroganov, 1962).

Condylobasal length of male skull (14) is 46.3–52.8 mm, of females (17), 40.0–47.1 mm; zygomatic width of males is 23.1–27.6 mm, of females, 19.0–24.2 mm; interorbital width of males is 8.8–12.2 mm, of females, 7.7–9.5 mm; mastoid width of males is 20.2–24.0 mm, of females, 17.7–22.2 mm, (Stroganov, 1962).

Length of os penis is 25-27.1 mm (Ognev, 1931).

Weight of Siberian solongoi males is up to 350 gm, of females up to 220 gm (Stroganov, 1962), usually much smaller. Males from Pribalkhash weigh 217-255 gm (January-March), females, 122-135 gm (Sludskii, 1953) (V.H.).

Systematic Position

Due to the known complexity and diversity of structure of genus *Mustela*, determination of the position of separate species presents difficulties. Of those forms of the genus which are accepted at the present time as independent species, *M. altaica* stands closest of all to the southern Asiatic (South China, Indochina, Himalayas) *M. kathiah*. It is sometimes considered, and is possibly true, that it is only a race of *M. altaica*. Relationship to the Malayan *M. nudipes* is insufficiently clear, but they are probably close.

Among our forms and in our literature, *M. altaica* is accepted, according to a tradition proceeding from Satunin, to be closest to the Siberian weasel, *M. sibirica*. This is emphasized by combining them into one subgenus (in extreme cases—one genus) *Kolonocus*. In keys for identification, both species, even in the most recent books, are found in one group (see note on page 1033).

Nevertheless, in actuality there is no particular relationship between the solongoi and Siberian weasel. The singular, or in all events the main common characteristic of both species was considered (as in keys) to be color. However, there are very essential differences in this characteristic. As shown (see above, section, "Description", and below, "Geographic Variation"), in the solongoi, color type itself is different, particularly contrast between dorsum and venter may be very strong, and the demarcation between one and the other is sharp. The general color tone in some forms [of altaica] is almost devoid of the characteristic ocherous-reddish tone. External similarity to the Siberian weasel is found in only one race of the species (M. a. raddei) and only in winter pelage.

At the present time, it is more correct to consider that the solongoi is, according to several external characteristics and craniological peculiarities, closer to ermine. It is necessary, however, to have in view that as a consequence of the significance of some race characteristics of our solongoi, not all of them are identical with them in this connection. Thus, *M. a. raddei* possesses all known characteristic similarities of the Siberian weasel, not only

691

in color but also in the craniological structure. With all of that, the solongoi is, in all events, closer to ermine than to Siberian weasel. According to the sense of some (Pocock, 1941), differences between solongoi and Siberian weasel are even larger than those between Siberian weasel and European mink (M. lutreola). This recital lead us to consider the order of species accepted here, i.e. the structure of the genus, as a more suitable natural relationship and refuse to accept the group Kolonocus in any form or rank, or in general any preference for affinity of solongoi and Siberian weasel within the genus Mustela (V.H.).

Geographic Distribution

The range of the species is relatively small and occupies montane, rarely level regions of Central Asia and adjacent parts of Middle Asia and Siberia, the Far East and China.

Geographic Range in the Soviet Union

In the USSR it is small, and represents the most northeastern, northern and northwestern fringe of the species range. It consists of several, in part very small, sections separated from each other within our country but united to the south, outside the border of the USSR. The details and even some of the essential features of solongoi distribution are still poorly known and the range cannot be outlined with sufficient accuracy.

In the west, the solongoi inhabits the Pamir, occupying both eastern and western parts of the region and the Trans-Alaisk and, apparently, the Alaisk range. The northwesternmost known point of occurrence in the Pamir is Lyangar in the upper Obikhonogoi (Vakhsh) in the northern part of the Darvaz range. In southern Tadzhikistan, in turgais along rivers flowing into the Pyandzh and Amu-Dar'ya, it is absent. Concerning its occurrence in the Peter the Great, Gissar and Zeravshan ranges, there are no direct references. At least in the latter two regions and along their western spurs, it is absent (in general not recorded within Uzbekistan; Ishunin, 1961). It is also, apparently, absent in the Turkestan range.

In the montane system of Tien Shan, the solongoi lives in its eastern part—in Kungei Alatau, Tersk Alatau and in Zailinsk Alatau, and in montane regions lying to the south as far as the Fergana

valley. In this valley the solongoi has not been noted; and is, apparently, absent there. The Tien Shan and Pamir sections of the range, are probably in the extreme eastern, montane parts of Fergana, but within the borders of the USSR may be isolated from each other.

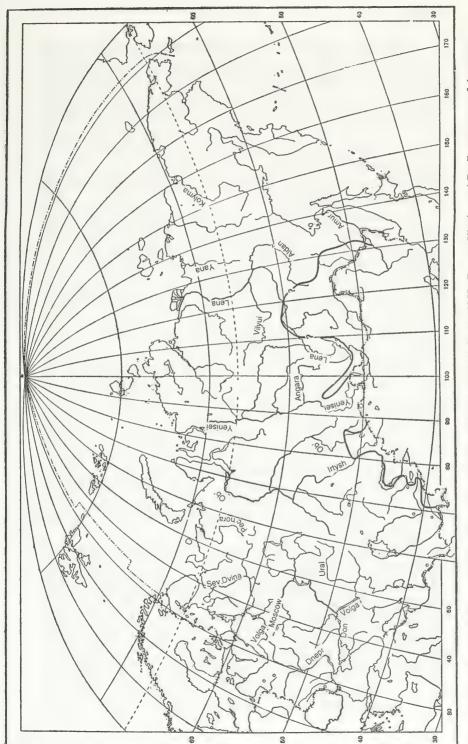
In the mountains of western Tien Shan (Kirghiz and Chatkal ranges, Talass Alatau), presence of the solongoi has not yet been recorded and it probably is absent there (Sludskii, 1953); mention of its sporadic occurrence "all over Kirghizia" (D. Dement'ev, 1938) and several others are too indefinite. It is encountered in the Dzhungarsk Alatau, in the lower Ili and Karatal, along the Lepsa and Aksu, along the southern shore of [Lake] Balkhash (in the east, recorded at mouth of Ayaguz) and in the Alakul' depression. Here, the occurrence of this montane species among tugais and reeds on the plain between deserts is remarkable.

Farther to the east, it lives in the Tarbagatai, Saur, in Zaisan depression and the mountains surrounding it, along the Chernyi Irtysh and in the Kalbinsk Altai (left bank of Irtysh).

In the Altai, the solongoi is known from a series of places—Sailyugem, Chuisk mountains and Chuisk steppe (Kosh-Agach) in the south, from the Ust'-Koksa, Uimon, Ongudai, Koop-Ching, Kotanda Elikmonar regions, and a series of other places, however, not to the east of the Katun'. The northern- and northeastern-most known point of inhabitation in the Altai—Turochak—lies, however, on the Biya (northeast of Gorno-Altaisk); reference to its occurrence around Barnaul applies, apparently, not to the city itself but to the Altai mountains south of it.

To the west of the Katun' the solongoi lives, apparently, all over the mountains and foothills as far as the Irtysh; it is met with in the south up to the frontier (Kurchumsk, Narymsk and other ranges), and in the north around Ust'-Kamenogorsk and extends to Semipalatinsk and it even penetrates somewhat farther north (Beskaragaisk region of Pavlodarsk district). In this way, the Altai region of occurrence is united with that of Turkestan in our country.

Deep in the eastern part of the Altai to the east from the Katun', the solongoi is, apparently, absent (Turochak lies in the northern foothills). Thus, it has not been discovered in the Altai preserve around Teletskoe Lake and along the right bank of the Chulyshman (Shapshal range; V.G. Heptner, Yurgenson, 1938). It is also absent along the West Sayan range and the mountains to the north of it, as well as in Tuva.



692 Fig. 248. Borders of the range of the solongoi, Mustela (Mustela) altaica Pall. in the USSR. Eastern Siberian and Far Eastern parts of the range are represented on the basis of a few fragmentary indications (see Fig. 249) V.G. Heptner.

In the literature, very general references to the occurrence of the solongoi "in Altai and in Sayan" are occasionally encountered, and sometimes, its occurrence in all of these montane regions is emphasized. As is apparent, in the Altai the picture is complicated, and as regards the western Sayan, not a single accurate positive record is found, but there is negative (Stroganov, 1962, after Nadeev). There are also no positive data concerning Tuva (Yanushevich, 1952, refers to it in this district with a question mark; see also the section "Geographic Variation" and notes on the Trans-Baikal solongoi).

The Cis-Baikal part of the range of the solongoi* west of [Lake] Baikal is represented by a quite narrow strip which, beginning from Achinsk and Irbeisk regions (east of Krasnoyarsk, about 95° E long. and 56° N. lat.), extends along eastern Sayan range to the southeastern corner of Baikal, including in particular, the Tunkinsk mountains and Slyudyank region on the east (southeastern extremity of Baikal); it continues onto Khamar-Daban (Podarevskii, 1936). Thence to the south, the range goes onto the boundary with the Mongolian People's Republic (Prikosogol'e).

If all existing information about the absence of solongoi in the western Sayan, in Tuva and in the extreme eastern parts of Altai, are true then, it is evident that these—the Eastern Sayan, Cis-Baikal and Trans-Baikal areas (see below) of the species distribution are cut off, within the borders of the USSR, from the Tien Shan-Altai part. At the same time, the reasons for this probable gap are not known, and the occurrence of the solongoi in western Sayan remains likely. However, the well manifested differences between the races of Altai and Trans-Baikal solongoi speaks against this (the eastern Sayan [race] is unknown; see below, section "Geographic Variation").

In Trans-Baikaliya, the solongoi is widely distributed. The eastern limit of the range here to a significant extent is served by the [eastern] shore of [Lake] Baikal. Southward the range extends beyond the state frontier, except that it also occupies the steppe regions of both southwestern and southeastern Trans-Baikaliya (for example, Aginsk steppe, the steppe expanses of Olovyannin region etc.). The distribution of solongoi to the north beyond Baikal is not well elucidated. Apparently, the range goes to the Lena, and

^{*} In Russian original, "kolonok," a lapsus-Sci. Ed.

perhaps somewhat beyond it, *i.e.* to 60° N. lat. and somewhat to the north (the northernmost place inhabited by the species). Thus, the solongoi is known (V.D. Shamykin) from the area along the Lena between approximately 111–112° and 120° E. long. The border of the range in the northwest between the northern extremity of Baikal and the Lena, is unknown.

The distribution to the east is also not accurately established. In the northeast, the solongoi is known from the Aldan (Tugarinov, Smirnov and Ivanov, 1934), apparently from its upper reaches, and in the south it undoubtedly reaches in the east the confluence of the Shilka with the Argun' and is recorded in the western parts of the Amur district (Plyater-Plokhotskii, 1936)²⁵.

For the distribution to the east of the meridian of the confluence of Shilka, Argun' and Aldan the literature contains only two positive indications—in the western part of Amur district and the neighborhood of Blagoveshchensk (Stroganov, 1962). In several works dedicated to the regions north of the Amur, this species is not referred to at all and is usually considered to be absent there. In actuality, the range apparently covers the whole expanse between the Amur and the Stanovoi range, perhaps without reaching it, but, occupying the upper reaches (and the sources) of the Zeya and Selemdzhya. From here, it descends abruptly to the south, occupying the lower Bureya and the southwesternmost (southern) part of the Bureinsk range²⁶.

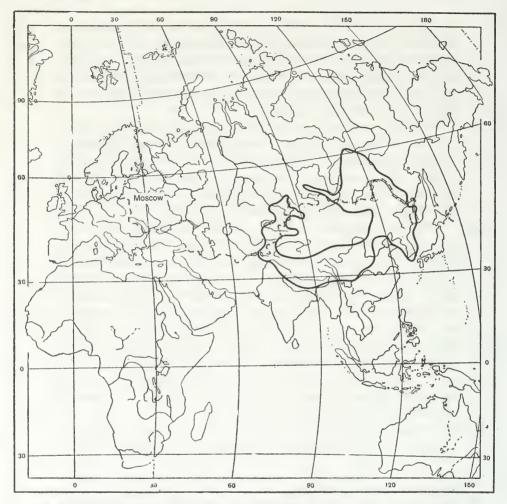
Including in this way the eastern slopes of the southern extremities of the Bureinsk range²⁷ somewhere a little to the west of

25In the description of the solongoi range east of Baikal, besides the sources mentioned, unpublished information offered by S. Anaskin (Bur[yat] ASSR), P. Zimin (Chita) and D. Ivanov (Yakutsk) were used. These available data are contradictory. Thus, for Chitinsk district, showing the solongoi distributed in the Krainii (Extreme) North in Yakutiya, its presence is denied. For Buryat ASSR, the northern border of the range is given as follows: from the eastern shore of Baikal at a place about 100 km. south of the mouth of upper Angara, to the source of the Barguzin, then to Baunt Lake and from it to the northeast, at first slightly to the south of the Mui river and to the Vitim to its mouth. Therefore, the northern and eastern borders of the outlined section of the range is preliminary and to a certain degree, conditional. They strongly differ from those advocated by other authors, notably Stroganov (1962).

²⁶The above described part of the range in the Priamur'e is given according to range maps made by A. Samsonov (Blagoveshchensk) and V.P. Sysoev (Khabarovsk).

²⁷Range in Primor'e after data (map) of P. Bel'skii and V.D. Shamykin. The solongoi is very rare everywhere. In the faunistic literature concerning the territory, the solongoi is nowhere mentioned. Therefore, it is possible that the range here is in

fact more restricted than was mentioned.



694 Fig. 249. Species range of the solongoi, Mustela (Mustela) altaica Pall. (V.G. Heptner).

132° E. long. or along it, the range border crosses the Amur and exits into China. It again enters the borders of the USSR in Primor'e, at the Bikin Basin in Ussuri. Thence, the range extends as a narrow strip southwards along the Ussuri valley and the adjacent western foothills of the Sikhote-Alin', and then, a bit south of the latitude of the southern extremity of Lake Khanka, the border turns slightly to the southeast and passes to the Ocean at Nakhodka.

Within the borders of our country, a clear break in the range is marked out along the Amur to the east of the Bureinsk range and along the lower Ussuri. However, it is not excluded that, in the 1043

Priamur'e, the solongoi goes to the east somewhat farther than mentioned.²⁸

Geographic Range outside the Soviet Union

This is only known in an entirely general outline. It occupies Kashgariya (obviously, montane parts contiguous to our country) and Dzhungariya, in the Mongolian Republic—Mongolian Altai and the eastern part of the Mongolian Republic from the Kentei to the Great Khingan [mountains] and south approximately to 46° N. lat. (in the region of the Great Western and Gobi lakes and in the Khangai as well as in the remaining parts of the country, the solongoi is absent). In the Korean Peninsula, it inhabits at least its northern parts. In China, the range occupies its northeastern part, extends eastwards to the middle parts of Shansi and to Hubei (apparently, to the Great Chinese Plain, from whence it is not recorded), and southwards to Sichuan, Yunnan and Fujian, as well as Tibet. In the south, the range includes the Himalayas from Sikkim to Kashmir, Ladakh and Gilgit, the Karakorum and the extreme east of Afghanistan (V.H.).

Geographic Variation

Within the borders of our country, the solongoi provides several well defined races. It is noteworthy that despite the relatively small territory occupied in our country by the range of the solongoi, the number of these races is quite large, and morphological differences, at least some, are significant. They are greater than in races of our ermine, even those inhabiting parts of the country that are remote from each other. The subspecies of solongoi represent also interesting combinations of characters together forming not only quantitative but also some qualitative differences. Due to the scarcity of material in our museums, geographic variation of the

²⁸Range in the USSR after Maak, 1859; Shrenk, 1859; Radd, 1862; Przheval'skii, 1870; Gassovskii, 1927; Emel'yanov, 1927; Kuznetsov, 1929, 1948, 1950; Ognev, 1931; Tugarinov, Smirnov and Ivanov, 1934; Flerov, 1935; Zolotarev, 1936; Plyater-Plokhotskii, 1936; Podarevskii, 1936; Favorskii, 1936; D. Dement'ev, 1938; Yurgenson, 1938; Kolosov, 1939; Razoprenova, 1939; Bobrinskii, 1944; Kopylov, 1948; Nasimovich, 1949; Yanushevich, 1952; Sludskii, 1953; Chernyshev, 1958; Afanas'ev, 1960; Ishunin, 1961; Stroganov, 1962 and other sources and according to unpublished material of S. Anashkin, D. Ivanov, G.F. Bromlei and V.G. Heptner.

696

solongoi is still, however, quite insufficiently studied. Within the USSR, the following forms now can be recognized from material of the Z[oological] M[useum] of M[oscow] U[niversity]; measurements of the Siberian forms are mainly from Stroganov, 1962.

1. Turkestan solongoi, M. (M.) a. sacana Thomas, 1914 (syn. birulai).

General color tone of upper body in the winter fur very light, straw-sandy-ocherous. Venter considerably lighter than dorsum, transition from color of back to color of belly gradual.

In summer fur, the color above is noteably darker than in winter, brownish-gray with light-chestnut and reddish tones. Bases of hair dorsum bluish-gray. Top of head darker than back (pale-sandy and smoky tints of underfur not present). Pure white, or with light straw-colored tints on lips, chin and upper part of throat washed away at edges, rarely sharply demarcated from color of throat and cheeks. Color of lower surface of the body (belly, chest and neck) very light, pale-straw or ocherous-white, in some animals almost white (bases of hairs often white) with yellowish or reddish overlay, particularly obvious on sides of neck. Dark color of dorsum extends to sides very sharply demarcated from light color of venter. Distal portion of feet silvery-white above. Tail moderately fluffy. On the whole, summer color is variable, but lighter than in other races (material from Issyk-Kul').

Body length of males is 224–282 mm, of females, 218–230 mm; tail length of males is 116–132 mm, of females, 90–114 mm; length of hind foot of males is 39–46 mm, of females, 34–35 mm; ear height of males is 16–20 mm.

Weight of males (winter) is 217-255 g, of females, 122-135 g (lower Ili, Pri-Balkhash; Sludskii, 1953).

Mountains of Middle Asia including Dzhungarsk Alatau, Pri-Balkhash.

Outside the USSR—probably in contiguous parts of Kashgariya, perhaps in Dzhungariya and Afghanistan.

It is a very sharply distinguished form (material from Tersk Altau), the lightest form within the USSR both in summer and in winter. In general tone of summer fur and contrast between dorsum and venter of the body it is very reminiscent of ermine.

Nomenclature of this form is not completely clear. It is undoubtedly (contrary to Ognev, 1931) well differentiated from the Altai [form]. The identity of the Tien Shan and Pamir solongoi

("birulei") is highly probable, but needs confirmation. On the other hand, it is probable that the Pamir and perhaps also the Tien Shan are related to the Himalayan form, temon. Their description is similar and there are analogies to such distribution found among other mammals. Therefore, the same sacana given to the Turkestanian montane solongoi is provisional.

The systematic position of solongoi of the river valleys in Pribalkhash'e is not studied, but its position in this race is sufficiently evident.

2. Altai solongoi M. (M.) a. altaica Pallas, 1811 (syn. alpina). Color of winter fur of dorsum darker than in preceding form, light ocherous-chestnut color, dull. Lower surface of body much lighter than dorsal. Transition between color of dorsum and venter gradual, but in some, it is demarcated by more or less distinct boundary. Tail is moderately fluffy, color as on back.

In summer fur, dorsal side dull and very dark-brown tone. Darkening along middle of back relatively stronger than in other forms. Venter considerably lighter than dorsum, dirty light-ocherous tone, sometimes with small brownish spots. Border between color of dorsum and venter sharp.

Body length of males (7), 235–M241–260 mm, of females (5), 217–M223–227 mm; tail length of males, 110–M129–145 mm, of females, 104–M108–113 mm; length of hind foot of males, 41.0–M44.1–47.0 mm, of females, 35.5–M37.2–38.4 mm; ear height of males, 20–M20.8–21.6 mm, of females, 15.7–M16.8–18.2 mm.

Condylobasal length of male skull (7), 51.2-M52-53.0 mm, of females (5), 46.8-M47.3-49.5 mm; zygomatic width of males, 26.2-M27.2-28.4 mm, of females, 23.2-M24.4-25.7 mm; interorbital width of males, 10.3-M11.3-12.6 mm, of females, 9.3-M 9.6-10.2 mm; mastoid width of males, 22.8-M23.3-24.0 mm; of females, 22.0-M22.4-23.2 mm.

In Altai.

Outside the USSR—western part of Mongolian Republic (Mongolian Altai).

A well characterized form, obviously distinguished from both eastern and western forms. Darkest form in USSR.

3. Trans-Baikal solongoi M. (M.) a. raddei Ognev, 1928.

In winter fur, dorsal color bright reddish-ocherous or pale-ocherous. Abdominal surface of body slightly lighter than back,

697

but also light-ocherous. On sides, transition from back color to abdominal color gradual. Tail bright similar to back and fluffier than other forms. In summer fur, color of dorsum dark-chestnut, but somewhat lighter than in Altai form (altaica); venter lighter than dorsum—ocherous-yellow, of quite intensive tone. Transition from color of dorsum to abdominal gradual, without sharp border.

Skull dimensions less than in forms *altaica* and *sacana*, somewhat more elongated and sturdy, with narrower interzygomatic region.

Body length of males (6), 249–M265–280 mm, of females (7), 222–M224–226 mm; tail length of males, 108–M129–144 mm, of females, 100–M106–117 mm; length of hind foot of males, 40.8–M42.3–44.2 mm, of females, 33.2–M36.9–43.8 mm; ear height of males, 17.4–M18.3–26.6 mm, of females, 16.0–M17.3–20.2 mm.

Condylobasal length of male skull (6), 49.5-M50.5-52.3 mm, of females (7), 43.0-M44.2-46.2 mm; zygomatic width of males, 25.7-M 26.6-27.3 mm, of females, 20.0-M22.6-24.5 mm; interorbital width of males, 9.3-M10.3-11.8 mm, of females, 8.1-M9.2-10.0 mm; mastoid width of males, 20.2-M22.5-23.8 mm, of females, 18.7-M19.0-19.4 mm.

In Trans-Baikaliya, southern Yakutiya, Priamury'e? and Ussuri Territory.

Outside the USSR, in eastern part of M[ongolian] P[eople's] R[epublic], and northeastern China.

The Trans-Baikal solongoi represents a very well characterized form. In winter pelage, it is the brightest and most beautiful solongoi. Summer pelage is a little lighter than in the neighboring Altai and somewhat similar to the fur of the Tien Shan; absence (weak development occurs rarely) of a sharp boundary on the sides between color of dorsum and venter is characteristic. Characteristics of solongoi of the western Sayan are not known, nor is the systematic position of solongoi of Ussuri Territory.

The sharp differences between Altai and Trans-Baikal solongoi confirm the opinion about the absence of the species in the eastern parts of the Altai and eastern Sayan. The differences mentioned between the eastern Baikal region (Trans-Baikaliya) and western (Tien Shan and Altai) solongoi and in general the outlines of the northern part of the range (see Fig. 249) make us think that, from the old southern parts of the range, the solongoi dispersed from the

southeast into Trans-Baikaliya, and from the south and southwest—into Turkestan and the Altai.

* * *

Outside the USSR, the form M. (M.) a. temon Hodgson, 1857* (syn. astutus. longstaffi) is usually recognized, from the Himalayas and Tibet.

Geographic variation in solongoi occurring outside the borders of our country demand reexamination, and nomenclature revised. Inclusion of "M. kathiah" (with the subspecies caparioccoi) in species M. altaica is rejected by the majority of authors (V.H.).

Biology

Population. Within the limits of its range, the solongoi is a widely distributed and usual, but uncommon animal. They constitute one of a few, except in the lower reaches of the rivers of southern Pri-Balkhash, where in years of abundant animals, along a route of 10 km there were 8–25 solongoi tracks.

Habitat. The most significant part of the range lies in montane regions where there is negligible development of forest vegetation and a predominance of open landscapes. Habitats of solongoi are extremely varied. They are, first of all, determined by interrelationships with the other small carnivores—by competitors. In Kazakhstan, competing species reveal themselves to be ermine, marbled polecat and kolonok. Kolonok and solongoi are two such inter-relating species. In many cases, they occupy similar habitats: valleys of montane streams and lakeshores in montane-taiga regions. In these cases, solongoi are usually restricted to subalpine and alpine zones, and kolonok to forest zones, the borders of which solongoi rarely penetrate, and then only where kolonok are absent (Sludskii, 1953).

In the mountains of Middle Asia, the solongoi is typical of altitudes from 1400 to 3000 m above sea level, inhabiting the shrubby valleys of montane streams, rock slides and talus covered with herbs, pebbly areas at the upper borders of spruce forests [scree slopes?] and other places (Shnitnikov, 1936; Sludskii, 1953).

^{*}In Russian original, "1957"-Sci. Ed.

In Tien Shan habitats, where there are many ermine, there are few solongoi and vice versa. In the vast areas of channels in the deltas of the rivers draining into [Lake] Balkash (Sludskii, 1953) which alternate with small lakes, salt flats, ridges and sandhills, the solongoi is most often encountered along the banks of small river channels and lakes, in small meadows with dense herbaceous cover and were rarely in tugai [riparian] forests. Sandhill, here are inhabited by the marbled polecat [Vormela peregusna].

In western Trans-Baikaliya, the solongoi is common in steppe and forest-steppe sections. In upland steppes, the solongoi is characteristic of hollows and ravines with mesophytic vegation (Fetisov, 1937). The same applies to places in southeastern Trans-Baikaliya (P.B. Yurgenson).

The solongoi does not avoid human proximity, settling in store-houses and dwellings.

Food. Rodents and birds of moderate and small size, lizards and in part, fish constitute the main food of solongoi. Cases of attacking domestic birds and stealing eggs and other food products are known.

Winter foods of the solongoi in western Trans-Baikaliya; rodents consists of 73.2%, birds—22.7% and insects—3.1% (97 spec.). Daurian pikas [Ochotona daurica] occupy first place in order of frequency (see Table 65).

The narrow skulled vole, Brandt's vole and Daurian pika predominate in the summer food of solongoi in southeastern Trans-Baikaliya (Brom, Vovhinskaya and Fedorova, 1948).

Table 65. Seasonal foods of solongoi in western Trans-Baikaliya (% of occurrence)

Type of food	Winter	Summer*
Daurian pika	34.2	27.2
Small birds	13.4	0.9
Brandt's vole [Microtus brandti]	9.3	27.2
Narrow-skulled vole [M. gregalis]	9.3	36.5
Daurian partridge[Pardix dauricae]	8.2	
Michnoe's vole [M. fortis michnoi]	6.2	,
Clawed jird [Meriones unguiculatus]	5.1	_
Large Asiatic wood mouse [Apodemus	5.1	_
peninsulae]		
Shrews	3.1	_
Daurian hamster [Cricetulus barabensis]	2.1	9.1
Fish	1.0	_

^{*}Summer food data after material from southeastern Trans-Baikaliya (Daurian steppes).

In Pri-Balkhash'e, the solongoi feeds mainly on voles and mice and in summer, to significant degree on lizards (Sludskii, 1953) (see Table 66).

Table 66. Seasonal foods of solongoi in Pri-Balkhash (% occurrence)

Type of food	Winter	Summer 66.6	
Mammals	61.0		
Rodents	61.0	66.6	
Voles, mice	24.2	25.2	
Muskrat	14.7	13.9	
Tamarisk jird. [Meriones tamariscinus]	10.5	5.5	
Midday gerbil [M. meridianus]	1.0		
Water vole [Arvicola terrestris]	5.8	8.7	
House mouse [Mus musculus]	_	11.1	
Tolai hare [Lepus tolai]		8.3	
Birds	5.2	11.1	
Pheasant [Phasianus colchicus]	_	2.1	
Moorhen [Gallinula chloropus]	_	5.5	
Ducks	-	2.7	
Small birds	2.1	2.7	
Lizards	_	22.5	
Frogs		2.7	
Fish	3.1		
Insects	_	8.3	
Coagulated blood	32.6	22.8	
Total data	95	36	

Home range. Data are absent.

Burrows and shelters. In the way of temporary burrows, and for rearing young, the solongoi more often use holes dug by rodents (water vole, muskrat, gerbil, pika). Therefore, the burrows of solongoi are often located near water and even on floating mats on lakes (Sludskii, 1953). The burrow usually has a nest chamber and also a "latrine". At its entrance, remains of food are often found. In the autumn—winter period, the solongoi has several temporary shelters within its home range in each of which it lives for some days in a row.

Daily activity and behavior. In summer time, the solongoi is active in twilight but is also met with during the day, i.e. its daily activity rhythm is imprecise (P.B. Yurgenson—Trans-Baikaliya; Sludskii, 1953—Kazakhstan). The solongoi is bold and has little caution. Being a typical terrestrial predator, it can also climb well and does not fear water. Its voice is a shrill chatter like that of ermine.

Seasonal migrations and transgressions. Data are absent.

Reproduction. Estrus and mating of solongoi in Kazakhstan are observed from the second half, rarely from the beginning, of January to the beginning of April.

The duration of pregnancy has been given as from 30 to 40 days. The number of young in a litter is from 1–2 to 7–8. The latest date of parturition was noted on 20 May (Sludskii, 1953).

According to more detailed investigations (Gusev, 1955), the first signs of spermatogenesis in individual animals (210 spec.) were observed at the end of December. In the first half of January, it was observed in all males. Extinguishing of the process extended from the second half of March to the first days of May. In individual old females, estrus appeared in the first half of February, and in the majority—in March. In young, estrus lasted from the second half of March to the first days of April. Parturition proceeded from the first days of April (old females) to 15–20 June.

700 Duration of pregnancy ranged from 30–35 days. The number of embryos was from 2 to 6; average for adult females was 5.5 and for young—3.6. Lactation period lasts 34–41 days.

Growth, development, and molt. Eyes of the young are opened after 27 days, probably at the age of 30 days. At the age of about 2 months, they already lead an independent mode of life, but the litter does not break up until late autumn (Sludskii, 1953).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Ermine, kolonok and marbled polecat are considered to be the main competitors of solongoi. Significant mortality (cause not established) was observed in 1941 (individual animals and litters) in Semipalatinsk district (Sludskii, 1963).

Fluctuation in numbers of solongoi are well expressed. In periods of depression, their number decreases 2-4 times and after that, restored in the course of 2-3 years. From 1936-1949, numbers of solongoi in Kazakhstan fell two-fold (Sludskii, 1953). In 1939, the sharp decrease in its numbers coincided with a strong tularemia epizootic among rodents. Numbers of solongoi are also, without doubt, affected by the vast spring fires in the delta of the Ili river. In southeastern Trans-Baikaliya, the picture is different. Here, there were four increases in numbers of solongoi within a 9-year period (1940-1948), after which followed deep depressions. The fluctuation was not 2-4-fold but 16-fold. Increases in numbers

repeated after 2-3 years (1940, 1943, 1945, 1948), and in a few cases, in the year, after an increase in numbers of rodents (P.B. Yurgenson).

Field characters. In nature, the solongoi differs from ermine (in summer) in denser, fluffier tail without a black tip. It differs from the kolonok in its smaller dimensions and paler color (P.Yu.).

Practical Significance

The significance of solongoi in fur trade is not great. In Kazakhstan, its catch constitutes 0.2% of the tanned fur. Nowhere is it hunted commercially. It is captured incidentally, but not specifically trapped. In the Balkhash region, the solongoi is harmful to commercial hunting, destroying muskrat and pheasant, and damaging the skins of muskrats in traps. Here, it may be considered a harmful predator.

In agriculture and for ecosystem health, it may be considered a useful animal since it destroys harmful rodents. However, this benefit is not great, since solongoi are encountered predominantly in uninhabited or weakly populated areas. For the same reason, the harm it causes by attacking domestic poultry is insignificant. In pre-war years in the USSR, about 50,000 animals were captured annually (Stroganov, 1962) (P.Yu.).

KOLONOK [SIBERIAN WEASEL]

Mustela (Mustela) sibirica Pallas, 1773

- 1773. Mustela sibirica. Pallas. Reise d. versch. Prov. d. Russ. Reiches, 2, p. 701. Tigeretsk Post near Ust-Kamenogorsk, Altai.
- 1844. *Mustela itatsi*. Temminck. Fauna Japonica, Mamm., p. 34, t. VII, Fig. 2. Japan.
- 1871. Putorius fontanieri. Milne-Edwards. Rech. Mamm., p. 205, pl. 61, Fig. 1. Pekin [Beijing], China.
- 1904. Mustela sibirica miles. Barret-Hamilton. Ann. Mag. Nat. Hist. 13, p. 391. Dauriya, Trans-Baikaliya.
- 1911. Mustela manchurica. Brass. Aus dem reiche der Pelze, p. 490. Manchuria.

- 701 1911. Kolonokus sibiricus australis. Satunin. Izv. Kavkazskoyo muyzeya, 5, p. 23. Zhiryakovo, Antropovsk. vol[ost]., Tyumensk county.
 - 1926. Kolonocus sibiricus coreanus. Domaniewski. Ann. Zool. Mus. Polon., 5, p. 55. Seoul, Korea.
 - 1934. Mustela (Kolonocus) sibirica charbinensis. Lowkashkin [Loukashkin]. China. J. Sci. and Arts, 20, p. 49. Krestov Island on Sungari river near Harbin, Manchuria (V.H.).

Diagnosis

General color monotone and evenly bright, ocherous-reddish or rusty-brown tones; venter same color as dorsum or slightly lighter; on sides dorsal color gradually merges into ventral coloration without noticeable boundary. End of muzzle and region near eyes coffee-brown ("mask"), and on lips and chin, a sharply outlined white area. Legs no darker than trunk. Postorbital constriction is elongated, its lateral outlines almost parallel, no distinct isthmus directly behind supraorbital processes. Dimensions relatively large—condylobasal length of male skull more than 55 mm, of female, more than 49 mm (V.H.).

Description

The kolonok has a long stretched-out body on relatively short legs; with, however, a general appearance of being heavier than solongoi, and especially ermine and weasel. In this respect, it seems to occupy an intermediate position between these forms and the larger members of the genus—mink and especially polecats. This is also associated with the relatively large measurements of the kolonok. The head of the kolonok is relatively small, narrow and elongated. Ears are broad at base, but not tall, and in winter, barely protrude from fur. Length of tail with terminal hairs constitutes about half of body length.

Winter fur very dense, soft and fluffy. Length of guard hairs reaches 30–40 mm; underfur dense and close-fitting. General color of entire animal monotone, bright reddish-ocherous or straw-red, sometimes, orange or peach tone noticeable on skin. This color especially bright on back, on sides a bit paler, somewhat paler yet on abdominal side. Neck and throat colored like abdomen, outer side of claws same color as dorsum of body.



Fig. 250. Kolonok, Mustela (Mustela) sibirica Pall. Sketch by A.N. Komarov.

On anterior part of head, covering the circumference of the eyes and forwards to the end of the nose, a dark coffee-brown sharply outlined spot—"mask". Upper and lower lips sometimes have light ocherous highlights. Their color sharply delimited both from dark color of mask and from adjacent ocherous-red areas. In some individuals, white color covers bare tip of nose in form of narrow band extending from sides and back [of head] or from sides only. Sometimes, one or several white small spots occur on throat.

702

Tail usually brighter than back—bright-red above and below. It is covered by long, dense, loose-fitting hairs and is very fluffy, fluffier than all other species of genus, including polecats and minks. Tail thickest of all in middle part, gradually thinning towards its base and rapidly coming to naught at tip, which is tapered. Lower part of paws covered by dense, elastic silvery-straw hairs, through which, however, callous digital pads located beneath the hairs show. Dorsal paw has same color as back.

In summer fur, whole trunk covered by shorter, coarse, quite close-fitting hairs. On tail, hairs relatively short, close-fitting; therefore it appears thin, of equal thickness along entire length.

Color almost completely monotone over whole body. General tone of back dark with intense ocherous-brown, and with middle of back only somewhat noticeably darker. Sides same color as back, ventral surface of body only slightly lighter than dorsal. Color of throat only slightly more intensive than abdomen. Upper side of fore legs often slightly darker than hind, which have color of sides. Tail, dorsally and ventrally, has same color as back.

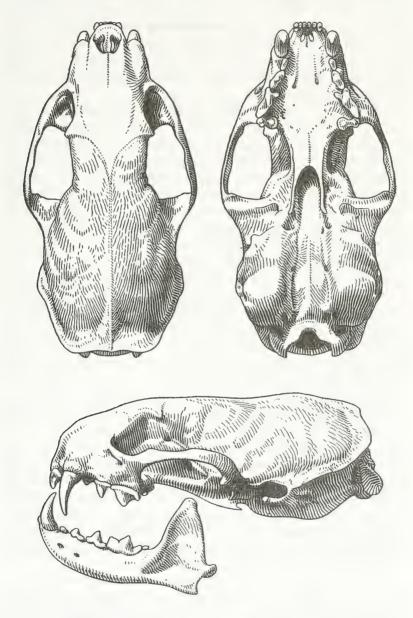
Lips (upper and lower), chin, and often narrow stripe around bare part of nose are a pure white or dirty-white color, or slightly ocherous, but always sharply demarcated from color of surrounding parts of body. Anterior part of muzzle darker than remaining part of head, but this "mask", in contrast to that in winter, is not so sharply limited; its posterior border is completely unclear and color of "mask" here gradually transitions to color of top of head.

Individual variation in color has small range, manifested in general tone, size and intensiveness of mask color and white field around mouth. Sexual differences in color are absent. Young animals are clothed in downy brown fur, darker than in adults. First winter coat does not differ from fur of adults. Geographic variation in color of kolonok within boundaries of USSR almost unexpressed or expressed very weakly and revealed only in some deviations in mean intensity of general color tone.

Among kolonoks albinos are encountered—complete or partial (Zalesskii, 1970), white with light red guard hairs on back and tail, and several other mutational variants. "Giant kolonok" mentioned below have color which is not normal.

The kolonok skull occupies, in several characters, an intermediate position between the skulls of ermine and mink. It is larger and more elongated than ermine and is somewhat flattened compared with the mink skull. In general outlines, the skull is narrow and elongated, considerably narrower and longer than solongoi, and the brain case is elongated and weakly swollen. Mastoidal width usually less than half condylobasal length of skull and significantly less than distance from anterior edge of foramen magnum to anterior point of interpterygoid notch. Region of postorbital constriction elongated, its isthmus almost unexpressed or weakly expressed, and outlines of lateral sides of this part of braincase almost or more or less parallel. If something of an isthmus can be noted, then it is not situated close to supraorbital processes. Its narrowest part is located away from the line uniting supraorbital

processes, not less than half the distance between the outer ends of these processes.



703

Fig. 251. Skull of the kolonok, Mustela (Mustela) sibirica Pall.

Infraorbital foramen less than alveolus of upper canine or equal to it. Interpterygoidal area does not have form of a forwardly directed angle, and does not evenly narrow anteriorly. Auditory bullae elongated, their width constituting about half their length or less. Distance between inner borders of anterior parts of bullae somewhat less than in posterior part. Distance between bullae in their anterior part less than width of hard palate at anterior edge of interpterygoidal notch.

Zygomatic width approximately equal to skull width in mastoid region or slightly more. Zygomatic arches elongated and weak. Protuberances, crests, etc. of skull relatively weakly developed, but generally stronger than in solongoi. Sagittal crest clearly noticeable in posterior part of cranium and in anterior, is weakly defined; occipital crest well developed. Upper profile of skull uneven; an elevation is noticeable on it in posterior part of cranium and prominence in frontal area (interorbital region) is obviously convex. From the frontal area, the line of the profile of the facial region descends steeply downwards.

Teeth, especially canines, relatively large and strong.

On the whole, the kolonok skull represents the skull of a specialized predator and does not itself bear the infantile characters known in the genus which characterize the solongoi or at least of some of its races. This also applies to weasel and ermine to a lesser degree. In some respects, the kolonok skull is even more specialized than the mink skull.

Age and sex differences of the kolonok skull have not been especially studied. Generally, they correspond with those mentioned for other members of the genus *Mustela* (see description of ermine). The female skull is considerably smaller than the male, somewhat lighter and with less defined protuberances, crests, etc. In young the cranium in the interzygomatic region, in particular, is more swollen. Individual variation of the skull does not exceed "normal" limits for other close species, except the weasel. Geographic variation of the skull, within the boundaries of our country, is not at all or is very weakly emphasized, and bears only a quantitative character (general measurements).

The structure of the os penis is typical of the majority of species in the genus—the distal end is bent upward in the form of a hook. Also characteristic are several bends in the basal shaft of the penis, in the distal part; thanks to which all of it is directed

somewhat upward. The quite large dimensions of the bone are characteristic-more than in the species described above, compared to the general dimensions of the animal.

In dimensions the kolonok is considerably larger than ermine and solongoi and approaches ferret and mink, but is somewhat inferior to them. Body length of males (47) is 280-390 mm, of females (38), 250-305 mm; tail length of males is 155-210 mm, of females, 133-164 mm; length of hind foot of males is 53.6-68.0 mm. of females, 48-52 mm; ear length of males is 22.0-29.5 mm. of females, 19.0-23.0 mm.29

Condylobasal length of skull of males is 58.0-67.3 mm, of females, 49.8-62.7 mm; zygomatic width of male is 28.7-35.7 mm, of females, 26.4–32.1 mm; interorbital width of males is 11.7– 13.9 mm, of females, 10.5-13.0 mm; mastoid width of males is 26.8-31.0 mm, of females, 23.0-27.0 mm.

Os penis length is 32.0-35.8 mm.

Weight of male is 650-820 gm, of female, 360-430 gm (Stroganov, 1962), and also less—male (probably juvenile) is 395– 485 gm, female—about 300 gm (winter materials of Z[oological] M[useum of M[oscow] U[niversity]).

In western Siberia (Barabin steppe), sometimes, but very rarely, giant kolonok occur with significantly larger dimensions than usual. If the length of a commercial skin of normal kolonok from the tip of the nose to the end of the tail with its terminal hairs reaches only 59-60 cm, then in giant animals, it ranges between 80 and 88 cm. As well, color varies greatly—undercoat in "giant" kolonok is 705 almost white (dirty yellowish-white or light-grayish), and paws and end of tail are dark-brown (Zalesskii, 1930; Zverev, 1931). Therefore, several characters of the steppe (white) ferret are well expressed in them. Apparently, this is not an "exotypic" mutation of the kolonok, but a hybrid between kolonok and steppe ferret (M. eversmanni). These individuals are obtained in the region where both species live not only in one territory but also in one and the same biotope. Their large measurements are, apparently, an illustration of heterosis. "Giant kolonok" are known only from skins

²⁹From other data (Zverev, 1931; western Siberia), body length of males (55) is 310-430 mm, often 350-370 mm, of females (60), 300-360 mm, often 260-310 mm; tail length of males (50) is 140-220 mm, often 160-210 mm, females (55), 130-210 mm, often 150-170 mm.

prepared as furs, and their skulls especially were not studied in detail. "Giant ferrets" are known in detail (see below) (V.H.).

Systematic Position

As already mentioned above (see section "Systematic Position"—in solongoi chapter), an adequate bases for affiliating kolonok and solongoi is absent, the more so as they do not happen to be considered the closest species in the genus, combined in one group as opposed to others, etc. Other qualities than in solongoi—color type (no contrast in color of upper and lower body either in winter or in summer) and its geographic and seasonal variability—are the essential indices of the deep differences between these species.

The closeness of features of kolonok to mink are without doubt. In purely morphological features, the kolonok obviously differs from ferrets (subgenus *Putorius*); however, information concerning hybrids between these species occurring in nature (see above) point to a close connection between these seemingly separate species. This is, once more, confirmation of the homogenity of the genus *Mustela*, and at the same time an example of the complicated inter-relationships of its species. It is difficult to array them all in successive order, and quickly becomes necessay to think about a quite complicated arrangement around a radial [pattern]. The order of species which is closer to the traditional one is adopted here as the most natural (V.H.).

Geographic Distribution

In Southeastern, Eastern and Central Asia, the southern and middle zone of Siberia and the Far East, and in the eastern European part of the USSR.

Geographic Range in the Soviet Union.

Vast, constituting the greater part of the northern half of the range, and occupies the southern and middle zone of Siberia and the Far East as well as the eastern European part of the USSR.

In the European part of the USSR, the range of the kolonok forms a projection having as its base the Ural mountains, and directed westwards. In the Urals, the northern border passes just below 63° N. lat. from whence it goes to the southwest through the southeastern and southern outskirts of Komi district to the source of the tributary of lower Sukhona—the Luza (Oparino to the northeast, and Letka and Ob'yachevo to the north of Kirov), where it passes below 60°20′ N. lat. (Ob'yachevo), and thence to the middle Vetluga. From here, the border line apparently passes generally along the Vetluga and Volga to Kazan, and then is directed to the southeast, covering a great part of Tatariya, the northern- and northeasternmost outskirts of Kuibyshev district and Bashkiriya, and passes onto the southern Urals³0.

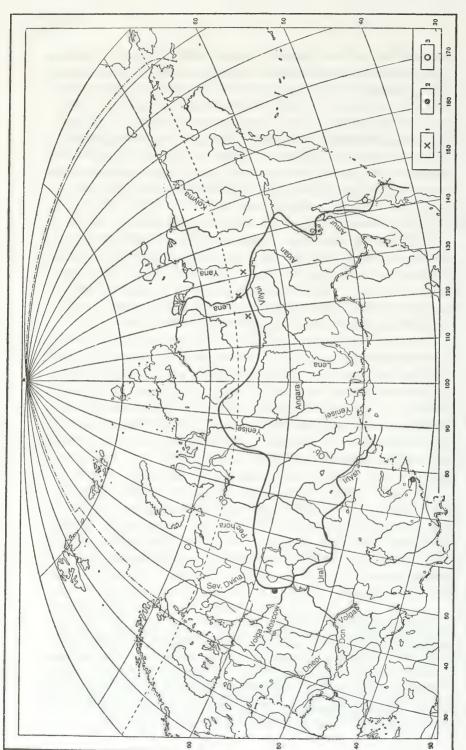
707

In the extreme south of the Urals, the kolonok is distributed over the whole montane region and is also encountered in the forest-steppe between the Sakmara and Ural (in the area between Kuvandyk and Saryktash') and even in the Guberlinsk melkosoposhnik [small hills] (the inner part of the angle formed by the winding Ural) to Guberlinskaya (somewhat westward of Orsk) and in the floodland of the middle course of the Ural.

In Siberia, the northern border of kolonok range from 63° N. lat. in the Urals, crosses the Ob' river, passes to the upper Pur and then suddenly ascends to the north on the lower Taz, almost reaching the Arctic Circle here or, perhaps, even a little beyond it. To the east, the border still ascends to the north, passes to the upper Turkhan and the upper Kheta, crosses the Yenisei between Dudinka and Potapov (above Dudinka) and passes east of Yenisei in the region of Khantaiskoe and Ketoi lakes (69° N. lat.). This is the northernmost confirmed point inhabited by kolonok.

Farther, the border, in an unclear way, suddenly descends southward and then, returning to the east, goes on to the border of Yakutiya approximately at 63° N. lat., and at that latitude, crosses the upper Vilyui in the region of the mouth of the Chona (Maak, 1859; D. Ivanov). Still more to the east, the border passes to the middle course of the left tributary of the Vilyui—the Markha (64° N. lat.) and reaches the Lena to the north of the mouth of the

³⁰According to V.A. Popov (Kazan), during the whole time of investigations in Tatariya, the kolonok was never found west of Chistopol'. This same author also considers that the animals which were caught in the Vetluga basin (Dryablovo, left tributary of the Vetluga—the Kaksha, Krasnye Baki; Formozov, 1935) were themselves not naturally occurring animals, but were kolonok introduced into the Vetluga basin. At the same time, data on catch of these animals (1927–1932) and the known data on introductions of kolonok into the Trans-Volga (Semenov city on the Kerzhenets—1937; Puzanov, Kozlov and Kiparisov, 1955) do not offer a basis for this assumption. From the 40's, kolonok were not observed in Gorki district.



706 Fig. 252. Borders of distribution of the kolonok, Mustela (Mustela) sibirica Pall., in the USSR (V.G. Heptner): 1-long distance transgressions to the north in Yakutiya; 2—place where kolonok were introduced for acclimatization; 3—place where the Japanese weasel, Mustela (Mustela) sibirica itatsi Temm., was introduced on Sakhalin.

Vilyui at 65° N. lat. Thence, it descends to the south along the right bank of the Lena valley, covering thereby the lower courses of its right tributaries and thus goes to the mouth of the Aldan. Along the Aldan, also covering the lower courses of its right tributaries, the border goes to the Allakh-Yun' River and along it, extends beyond the border of Yakutiya (D. Ivanov). From the Allakh-Yun', the boundary passes to the mouth of the Okhota at the Sea of Okhotsk (about 59°10′ N. lat.; V.P. Sysoev).

Individual cases of captured kolonok, apparently, dispersing individuals, were recorded in Yakutiya and somewhat northward of the above-mentioned line—along the Tyung in its upper course, along the Lena in the direction of Zhigansk and somewhat northeast of the mouth of the Aldan.

South of the specified line, the kolonok is distributed through all of Siberia, and in the expanse extending from the Pacific Ocean to the southern Altai its range passes beyond the southern frontier of the state. It is absent only in the south of southeastern Trans-Baikaliya, and particularly south from the line going from the Argun' a little south of Nerchinsk Zavod, across the Kalga to Borzya, to Olovyannaya, and then to the left bank of the Onon, and thence southwest to the state frontier. In southern Altai, the kolonok extends south to the latitude of Markakol' Lake, but is absent in the Zaisan depression.

To the west of the Altai, the kolonok is met with in the Kalbinsk Altai (left bank of the Irtysh), but farther south the border goes north again, generally along the Irtysh, although south of Semipalatinsk, the kolonok is encountered locally on its left bank (Zharminsk region, for example). Farther, in northern Kazakhstan, the animal exists in the northern part of Pavlodarsk district (Irtysh region below Pavlodar) and in Severo-Kazakhstansk district, it is met with among the insular forests of Kokchetav and even the former Akmolinsk district. South of here, it penetrates to the area a little to the north (Alekseev forestry) and even a little southeast of Tselinograd (Vishnevsk region). Farther, the range boundary includes the northern and western parts of Kustanai district (east of Tobol), and proceeds to the Ural [river] in the Orsk region.

On the Shantar and Kuril islands, the kolonok is absent. On Sakhalin, fossils of Siberian weasels were also absent, but in 1932, the Japanese weasel was introduced to this region, and from that time, a quite permanent population has, apparently, been founded in Sakhalin, at least in the south.

The range of the kolonok in the last century has undergone considerable changes and in a series of places these changes are continuing at present. In several places in central Siberia, Yakutiya and the Far East, the kolonok is extending its range, though not very intensively. Particularly notable is the kolonok's colonization westward. Thus, even in the 70's and 80's of the last century it was absent in the Urals. The kolonok occupied the whole European (Cis-Ural) part of its range, *i.e.* a very significant territory, only in the present century. In the northeastern part of Tatar ASSR, it appeared around 1910. On the Vyatka, in Kirov region, it was first noted in 1926; in 1927 it penetrated to the eastern parts of Gor'ki district (Vetluga basin); it was rarely encountered on the sources of the Luza—right tributary of the lower Sukhona, and by 1949 it became "almost common" here (Ob'yachevo, Letka).

In some places, in a wide belt along the periphery of the range, sharp fluctuations in the boundary and numbers were noted in kolonok. This particularly applies, apparently, to the westernmost part of the range, where the distribution of Siberian weasel is sporadic, the greater part of the boundary is not only very badly understood, but is evidently also in general little defined and subjected to strong fluctuations. Thus, for example, in Perm district, lying within the border, it is found everywhere, except in the northwesternmost part. Up to 1925 the animal was very rare in the Tatar Republic. Then in 1925–1928 it became a mass [abundant] species and noticeably spread to the west, but in the 40's it again became rare. In Gor'ki district, appearing in 1927, the kolonok declined in the course of several years, and again disappeared, and since the 40's has not been recorded.

In Novosibirsk district, the kolonok was found in all regions up to 1940, but in 1955, the southwestern boundary of its range extended from Ust'-Tara on the southeast to the northern part of Lake Chana, and thence, arching towards the north to Kochka region which lies southwest of Novosibirsk. In northern Kazakhstan, it appears rarely, and transgressions do not occur every year, then becomes more common, inhabiting the territory and being caught regularly, and again completely disappears for years. These fluctuations in the range boundaries of the kolonok in Kazakhstan—

in Kustanai district and Tselinograd territory are, apparently, very sharply expressed.³¹

The boundary and numbers, apparently, change noticeably along the Irtysh. Therefore, the outlined range is maximal, and includes also areas of transgression and greatest movements.

Colonization was particularly intensive, first of all, in the European part of the USSR in the 20's, and perhaps the beginning of the 30's. Later, it weakened, and ceased; the boundaries of the range more or less stabilized, and in some places, it again decreased. Apparently, the situation was also nearly the same in southern Siberia and in Kazakhstan. It is possible that in western Siberia, there were also local extensions of the range boundary to the north; however, data about this are absent.

It is possible, apparently, to think that the previous colonization of the kolonok, which was observed in the past decades, as a continuation of a process begun much earlier. This belief lacks supporting data, but it is probable that the kolonok colonized Siberia, or at least its more northern parts, in the past century. This is indirectly shown by the characteristics of its range, which poorly fits into the usual landscape-geographic framework, and by several other circumstances, in particular weakly expressed geographic variation. However, there is no basis (Laptev, 1955)³² for considering that the kolonok was generally absent in western Siberia in the 18th century and that it was only found east of the Yenisei (Bobrinskii, 1946).

³¹This phenomenon is also well expressed in several other species, the southern distribution boundaries of which extend south to western Siberia and northern Kazakhstan.

³²The described range of the kolonok differs significantly from that which is usually described and illustrated (Bobrinskii, 1944 and others). This particularly applies to the boundaries of the range in Siberia. In particular, it is sometimes shown that the kolonok is distributed "over all of Yakutiya," its occurrence near Verkhoyansk is also mentioned.

In composing notes on the range, the following works were used: Maak, 1859; Shrenk, 1859; Sabaneev, 1874; Kashchenko, 1898; Ognev, 1931; Tugarinov, Smirnov and Ivanov, 1934; Adlerberg, 1935; Formozov, 1935; Heptner, 1936; Podarevskii, 1936; Lavrov, 1946; Kuznetsov, 1948, 1952; Popov and Lukin, 1949; Shvarts, Pavlinin and Danilov, 1951; Kirikov, 1952; Sludskii, 1953; Kiparisov, 1955; I. Laptev, 1958; Parovshchikov, 1959; Afanas'ev, 1960; Stroganov, 1962; Puzanov, V. Kozlov and a series of other authors. Chief among those providing original material can be selected V.N. Skalon (West and Central Siberia), P. Zimin (Chitinsk district), Bel'sk (Primor'e Territory), A. Samsonov (Amur district), S. Anashknin (Buryat ASSR), D. Ivanov (Yakutiya) and V.P. Sysoev (Khabarovsk Territory). In particular, through these materials, the whole boundary in Siberia was revised. V.A. Popov (Tatariya) and S.P. Chashchin (Perm district) provided their data on the European part of the USSR.

Kolonok were introduced for the sake of acclimatization in 1937 in the Semenov region of Gor'ki district (individuals from West Siberia) and in 1941, was introduced near Przheval'sk (Dzhetyoguz region, Chu-Bulak ur.,* individuals from Krasnoyarsk Territory).

709 Geographic Range outside the Soviet Union

This is vast, with complicated outlines, but still poorly studied. The kolonok exists in the Mongolian Republic, where it occupies



Fig. 253. Natural species range of kolonok, Mustela (Mustela) sibirica Pall. V.G. Heptner.

^{*}Contraction for urochishche, meaning "small village"—Sci. Ed.

northern montane region—Pri-Kosogol', Khangai and Kentei; on the Korean Peninsula and in China—northeastern (former Manchuria), and to the south including Guandong and Yunnan, in Tibet, in the Himalayas, to the west including Kashmir, and in Nepal and upper Burma. It exists on the Japanese Islands*, Taiwan and Java**.

There is no information about the occurrence of the kolonok in Indochina, and therefore the range of the species shows a strong and complete disjunction—south China and upper Burma on one side and Java on the other. That is how it is usually described (Pocock, 1941; Ellerman and Morrison-Scott, 1951). It is possible that this questionable gap is filled by other forms, which are considered separate species, in part, possibly, *M. nudipes*, which is close to *M. sibirica* and which inhabit Malacca, Sumatra and Kalimantan (Borneo). The elucidation of the actual picture demands further investigation, not only on the faunistics of Southeast Asia, but also the systematics of the kolonok (V.H.).

Geographic Variation

A series of forms have been described for kolonok, among them including some from our territory or neighboring territories. At the same time, as shown by the large collection materials Z[oological] M[useum of] M[oscow] U[niversity], geographic variation of the species within the borders of the USSR, *i.e.* the vast area extending from the Volga Basin to the Pacific Ocean, is very small—a small number of real forms and amplitude differences in characters is insignificant. This leads us to think that variation in the species is generally insignificant, and its presentation is exaggerated (Ellerman and Morrison-Scott, 1951).

The scheme recently suggested for our territory (Stroganov, 1962) is extremely fragmented and is mainly based in part on exceptionally subtle characters, the reality of which is highly doubtful. The recognition of the concept *natio* (for the form *australis*), which in essence is lacking in real content, does not make it more convincing. In exactly the same way, separation of the form *itatsi* into an independent species (see below) is also not well founded.***
Geographic variation in our kolonok is considered very insignifi-

710

^{*}Considered by some to be a distinct species, M. itatsi-Sci. Ed.

^{**}Considered by most to be a distinct species, M. lutreolina—Sci. Ed.

^{***}Contradictory?—Sci. Ed.

cant even by furriers (Kuznetsov, 1941). Several East Asiatic insular forms, in particular *itatsi* are better distinguished* in natural conditions of occurrence outside our country.

Within the borders of our country, two forms may be distinguished.

1. Siberian kolonok, M. (M.) s. sibirica Pallas, 1773 (syn. australis, miles).

Measurements comparatively small. Color of winter fur not vey bright, yellowish-red.

Condylobasal length of male skull (33) is 58.0-M61.7-63.5 mm, of females (15), 49.8-M52.8-56.3 mm; zygomatic width of males is 28.7-M32.2-35.2 mm, of females, 26.4-M27.8-29.6 mm; interorbital width of males is 11.7-M12.5-13.2 mm, of females, 10.5-M11.0-12.2 mm; mastoid width of males is 26.8-M27.5-28.7 mm, of females, 23.0-M24.3-26.1 mm.³³

Found in eastern European part of the USSR and in all Siberia eastward to Zeya basin.

Outside the USSR—found in the part of the Mongolian Republic contiguous to its range and, possibly, in extreme western parts of northeastern China (former Manchuria).

In some parts of the range, there can be noted a tendency towards deviation in the character (quality) of the fur coat (density, softness) and in its color (West Siberian lowlands, Yakutiya, Bashkiriya). These deviations are more noticeable in Trans-Baikaliya, where kolonok are somewhat brighter and, apparently, themselves represent a transition to the next form. All these deviations, even those in the Trans-Baikal population are, however, weak and their territorial limits are not clear and do not offer a basis for separation of independent geographic forms.

2. Far Eastern kolonok, M. (M.) s. manchurica Brass, 1911 (in our literature, the name coreana is accepted).

Average measurements somewhat larger than in nominal form; color lighter, red.

711 Condylobasal length of male skull (16) is 63.8–M65.4-67.3 mm, of females, 57.2-M61.2-62.7 mm; zygomatic width of males is 32.3-M34.3-35.7, of females, 27.0-M30.5-32.1 mm; inter-orbital width of males is 12.3-M13.2-13.9 mm, of females,

^{*}Contradictory?—Sci. Ed.

³³Measurement of this and the next forms from Stroganov (1962). Body measurements given above (p. 1057), from Zverev (1931), belong to this form.

11.0-M12.7-13.0 mm; postorbital width of males is 13.2-M13.6-14.0 mm, of females, 12.0-M12.7-13.3 mm; mastoidal width of males is 28.2-M29.5-31.0 mm; of females, 24.0-M25.0-27.0 mm.

This form is found in Priamur'e to the west to Zeya [river], Primor'e.

Outside the USSR—in northeastern China (former Manchuria), precise limits unknown.

A well defined form. Apparently, identical to the Manchurian [form] and must carry the name recognized here. Comparison of our Far East kolonok with Chinese and Korean, the names of which might be applied to ours (see synonymy) has not, however, been made and thus, the name *manchurica*, therefore, conditionally applied. It is probable that the name *fontanieri* may be more proper.

3. Japanese, or Sakhalin, kolonok³⁴, M. (M.) s. itatsi Temminck, 1844.

Measurements somewhat smaller than in Far Eastern kolonok, M. (M.) s. manchurica. Color of ventral surface of body somewhat lighter than dorsal, limbs slightly darker than trunk.

Skull form as in other races, but frontal area somewhat more bulging, inner border of auditory bullae somewhat separated posteriorly, and distance between auditory capsules in their posterior part is notably more than anterior. Part of hard palate lying behind the [last] molar somewhat narrower than in other races.

Body length of males (9) is 510-550 mm, of females (2), 341-465 mm; tail length of males is 145-165 mm, of females, 93-101 mm; length of hind foot of males is 57-65 mm, of females, 39-46 mm.

Condylobasal length of male skull is 57.2-61.9 mm, of females, 47.6-57.9 mm; zygomatic width of males is 31.3-33.2 mm, of females, 28.9-32.0 mm; interorbital width of males is 12.0-12.8 mm, of females, 9.1-12.0 mm (after Stroganov, 1962; supplemented by material of Z[oological] M[useum of] M[oscow] U[niversity]).

Found in Sakhalin, only in south. Acclimatized there in 1932. Outside the USSR—in the Japanese Islands (Hokkaido, Honshu, Shikoku, Kyushu, Iki).

³⁴It was suggested (Pereleshin, 1957; Stroganov, 1959, 1962) that this form be given the name "itatsi" for us. This name must be decidedly rejected. There is no reason at all to litter the Russian language with a word completely alien to it, especially a non-declinable one.

A well-distinguished form, differing more strongly from named forms than the latter do from each other.

Note. The relatively sharp differences between Japanese kolonok and Siberia turned attention to it when first recorded within the borders of the USSR (Pereleshin, 1957). Somewhat later, Stroganov (1960, 1962) decisively affirmed that the form *itatsi* is itself an independent species differing from *M. sibirica*. According to the words of this author and the majority of characters noted by him (12 in all), in particular, 5 out of 9 of which are craniological, a "sharp hiatus" exists between the form *itatsi* and those of the mainland.

Materials in the Z[oological] M[useum of] M[oscow] U[niversity] from Sakhalin (collected by A.I. Gizenko), however, show that the features distinguishing the form itatsi from Siberian are far from such as those described and illustrated by Stroganov (1960, 1962). A clear hiatus between is absent in any one. All are either not developed or are extremely variable and broadly overlapping. In particular, differences mentioned as of fundamental important and striking—position of the anterior edge of the auditory bulla in relation to the articulated groove (anterior edge of bulla found a distance half the bullar length from the articulated groove in *itatsi* and at a distance of one-fourth its length in *sibirica*) as well as dimensions and form of the bulla—are not demonstrated 712 at all in material of ZMMU. The same applies to other [characters]. Some bulging of the frontal area is noticeable (weak) and a well expressed difference in the position of the inner outline of the boney auditory bulla, as mentioned in the diagnosis above. Therefore, to believe that the form itatsi inhabiting Sakhalin is an independent species is without foundation. It is a true kolonok and its somewhat greater differences are, apparently, explained by its insular origin. The conclusions of Stroganov (1960, 1962) were based, apparently, on accidentally selected, atypical materials.*

Data on color dimensions could not be verified and are after Stroganov (1962). They require re-examination. The structural peculiarity of the posterior region of the hard palate was not mentioned earlier.

* * *

^{*}Recent work now supports Stroganov's opinion-Sci. Ed.

Outside the borders of our country, the following forms are usually mentioned:

1) M. (M.) s. subhemachalana Hodgson, 1837—Himalayas from Nepal to Bhutan; 2) M. (M.) s. canigula Hodgson, 1942—Tibet; 3) M. (M.) s. hodgsoni Gray, 1843—Kashmir and western Himalayas from Kam to Garwal (Garhwal); 4) M. (M.) s. davidiana Milne-Edwards, 1871—Southeast China north to Hubei, Taiwan; 5) M. (M.) s. fontanieri Milne-Edwards, 1871—Northern China, Shandong, Chihli, Shansi and Shensi; 6) M. (M.) s. moupinensis Milne-Edwards, 1874—Sichuan, Gansu and Yunnan in China; Burma; 7) M. (M.) s. manchurica Brass, 1911—Manchuria; 8) M. (M.) s. coreana Domaniewski, 1926—Korean Peninsula; 9) M. (M.) s. charbinensis Loukashkin, 1934—Manchuria; 10) M. (M.) s. quelpartis Thomas, 1908—Quelpart Island in East China Sea; 11) M. (M.) s. sho Kuroda, 1924—Tanageshima and Yakushima islands (southern Japanese archipelago) [= Ryukyu]; 12) M. (M.) s. asaii Kuroda, 1943—Oshima Island, Japan.

The list given is obviously inflated, probably approximately twice. For some forms, deviations in characters of the facial pattern, the majority of which are fairly variable, small differences in color intensity etc. are considered to be diagnostic characters (V.H.).

Biology

Population. The range of the kolonok is very extensive, but it exists in entirely different densities in relation to the great diversity of landscapes and, consequently, conditions of habitation. Figures of [fur] preparation do not reflect these particularities. The southern regions of Siberia and the Far East are richest in kolonok. The latter produces more than 1/3 of the skins prepared in the USSR. In the Gorno-Altai Autonomous District, the highest frequency of tracks found (in 10 km) in a series of years ranged from 2.85 to 6.6, and the lowest—from 0.01 to 0.22. In the taiga of the Sikhote-Alin' range, the number of tracks encountered along a 10-km route ranged from 24.1 to 38.8 in half the cases, but sometimes it decreased to 2.1 (Yu.A. Salmin and V.D. Shamykin).

Population and distribution of kolonok are determined by food abundance (mouse-like rodents and water voles), the stability of stocks, interrelationships with competitors (in dark coniferous taiga—with sable; in taiga river valleys—with ermine and also

American mink; at the upper edges of forests—solongoi and ermine; at the steppe border—with steppe polecats) and also the characteristics of snow cover.

Habitat. Kolonok habitats are varied. In the taiga, it willingly holds to valleys of forest rivers and creeks with dense thickets as well as the rocks and rock slides overgrown with bushes, forest marshes (sogra) and, after old burns, dense growth of saplings.

In the Altai mountains, the kolonok prefers dark coniferous taiga with larch stands. However, these are secondary habitats whence it penetrates after the extermination of sable, and from which after a time sable again crowd them out. In spruce-fir forests of the Sikhote-Alin' range, the kolonok is most numerous in mixed nut pine broad-leaved taiga, broad-leaved forests of the Manchurian



Fig. 254. Mountain creek—typical habitat of kolonok. "Kedrovaya Pad'" preserve, southern Primor'e. October 1963. Photograph A.G. Pankrat'ev.

713 type and in coastal oak forests. It is met with from the sea coast to the upper limit of the forest, but in the latter, it is rare.

In the forest-steppe of Siberia and the Far East, the kolonok inhabits birch and aspen clearings, reed thickets—"flood-lands" along the banks of steppe lakes and rivers, and meadow steppes with shrubby growth, and rarely—pine forest islands. It penetrates the depths of the taiga immediately after agricultural developments and human settlements, which is explained by concentrations of mouse-like rodents in these places. It often inhabits villages and even cities where on the one hand it destroys mice and rats and on the other causes damage to domestic fowl. It avoids open places.

Food. According to type of food, the kolonok belongs to a group transitional between the typical mouse-predators (weasel) to the polyphagous predators (true martens). Cold-blooded vertebrates, invertebrates (insects and molluscs) and plant food are not a consistent element in its ration and are not encountered everywhere. Rodents of small and moderate size constitute the basis of

Table 67. Geographic variation in foods of kolonok (% of occurrence)

714

Type of food	Tatar ASSR (Grigor'ev and Teplov, 1939)	Forest-steppe, western Siberia (Zverev and Klimov, 1931)	Taiga regions, western Siberia (Lavrov, 1937)	Northeastern Altai (Shaposhnikov, 1956 and Stroganov, 1962)	Northeastern Kazakhstan (Lavrov, 1937)	Forest-steppe, western Trans-Baikaliya (Fetisov, 1936, 1937, 1942)	Taiga, Primor'e (Yu.A. Salmin, V.D. Shamykin)
Water vole [Arvicola terrestris]	36.6	56.1	46.0	1.8	7.0		
Small voles and mice	15.0	15.6	15.0	50.1	20.0	24.6	68.7
Altai zokor [M. myospalax]				_	21.0	_	_
Great jerboa [Allactaga major]	_	_	_	_	14.0	_	_
Siberian chipmunk [Tamias sibiricus]	_	-	_	0.9	_	9.6	
Pikas	_	_		2.7	_	38.2	
Insectivores	6.6	0.8	_	33.8	2.0	3.5	-
Birds	3.3	4.6	15.0	6.4	29.0	13.6	9.4
Fish	13.3	-	15.0	_		0.5	4.4
Carrion	_	1.7	nelpodents	_	_		10.1
Amount of data examined	60	130	43	108	52	406	684

kolonok food everywhere. Species composition and ratio of each species depend upon the local conditions and competitive relationships with other carnivores. Geographic variation in primary



714 Fig. 255. Bank of a montane creek—characteristic winter habitat of kolonok. "Kedrovaya Pad'" preserve, southern Primor'e. March 1964. Photograph A.G. Pankraev.

(occurrence from 15% of cases) and secondary (occurrence from 5%) of foods is shown in Table 67 for seven different regions in the range. In it are placed only those foods and groups were given which were found, at least in one case, with an occurrence higher than 5%.

In the western part of the range, the main food is shown to be the water vole (Tatariya, western Siberia), and in the eastern—voles and mice. In the east, a number of main foods include rodents of moderate size—Daurian and Altai* pikas [Ochotona daurica, O. alpina], Altai zokor [Myospalax myospalax], locally, chipmunk and muskrat, and also squirrel [Sciurus vulgaris] (especially during migration periods of the latter) and jerboas. In different seasons, fish are of great importance in some places. In Ussuri

^{*}In the Russian original, this word is spelled "Alaiskaya", but this region is west of the one being discussed, and "Altaiskaya" was probably meant—Sci. Ed.

territory, carrion—food remains from wolf and yellow-throated marten—are very important in winter. Everywhere, birds play an essential role in food of kolonok, chiefly small ones—to a lesser extent, poultry. Attacks on domestic birds are a widespread occurrence, as is damage to trapped hares, squirrels, kolonok and other animals. Feeding on reptiles and amphibians is observed at the periphery of the range—in Tatariya and especially in Primor'e. Among a number of plant foods are found nut pine, "nutlets", fruits of actinidia vines and others. However, in the montane taiga of the Altai, the kolonok does not feed on nut pine "nutlets" at all (Ternovskii, 1956). In years with low numbers of mouse-like rodents, it suffers from hunger and eats carrion.

The dynamics of seasonal nutrition are known only for the mountains of Sikhote-Alin' and northeastern Altai; in other cases, there are data only for the winter period. In Ussuri territory, the main food throughout the whole year consists of mouse-like rodents. Carrion is eaten from November to March; birds—in June–August, and fish—in September–October (migration of salmonids).

715 The role of plant food (not above 4.9%) increases in August—February. Amphibians, reptiles and invertebrates are foods of the warm period of the year. The frequent occurrence of pikas (25%) is characteristic of the food of the Altai kolonok in the summer period.

The character of foods varies quite noticeably not only in different geographical regions, but also in different habitats. In the Sikhote-Alin mountains, the significance of carrion ranges from 0 to 20.8%, of birds—from 5.4 to 12.4%, plant foods—from 1.0 to 8.0%, etc. (food was studied in 12 habitats; Yu.A. Salmin and V.D. Shamykin).

The proportions of other foods change from year to year. In Tatariya, the proportion of fish sharply increases in years of reduced occurrence of few water-and small voles (to 33%) (Grigor'ev and Teplov, 1939). The kolonok eats about 100–120 gm of food per day (Uspenskii, 1933). The kolonok usually makes a store of food, which sometimes happens to be quite significant—up to 16 striped field mice [Apodemus agrarius] (Fetisov, 1936).

Home range. Apparently, the home range of the kolonok is quite considerable, since it moves from 1.5–2 to 6–7 km per day, and even up to 8–10 km. In the northeastern Altai, the area of daily activity constitutes 1.5–2.0 km² while the home range is equal to 4–5 km².

Burrows and shelters. Shelter chosen by the kolonok is varied. It may be a hollow in old fallen logs, empty stumps, piles of brushwood, space under the roots of fallen trees and under logs. The kolonok also often inhabits burrows of other animals (chipmunks, water voles, pikas and others), widening and deepening them. In western Trans-Baikaliya, the length of burrow passages of kolonok appear to be from 0.6 to 4.2 m, and depth—from 0.2 to 1.3 m. The nesting chamber is located in the middle or at the end of the passage, and is lined with bird feathers or wool of mouse-like rodents (Fetisov, 1936).

Within the boundaries of its home range, the adult kolonok has, beside the permanent burrows, up to five temporary shelters situated at a distance of several kilometres from one another (Fetisov, 1936).

Daily activity and behavior. Crepuscular and nocturnal activity is typical of kolonok, but its rhythm is not clearly expressed—diurnal activity of kolonok is a quite common phenomenon, especially in summer and autumn. It hunts in the morning and during the day, as well as in winter when severe frost occurs at night and during the day warms up (Shaposhnikov, 1956). During times of severe frost and snow-storms, the kolonok does not venture out of its snow shelter for a series of days. In the forest-steppe of western Siberia, this period of very low activity falls at the end of December–first half of January (Velizhanin, 1931).

The length of its daily tracks in winter in western Trans-Baikaliya (Fetisov, 1936) ranges from 3-4 to 8 km; in western Siberia and Kazakhstan (Sludskii, 1953)-to 10 km and more, and in the northeastern Altai-from 1.5-2.0 to 6-7 km. Its length depends on the quantity of prey and condition of snow cover (Shaposhnikov, 1956). In contrast to sable, in winter the kolonok hunts food more actively, mainly under the snow-under logs, in windfalls and beneath the arches of snow-laden bushes while sable more often lies in wait like a cat. Compacted snow and frozen crust makes hunting under the snow almost impossible for the kolonok, and therefore, it confines itself to the northeastern slopes of montane taiga in the Altai, and terraces of the northern quadrant, where the snow is always loose and where frozen crust does not form (P.B. Yurgenson). During one night, the kolonok enters into the snow more than 30 times during a distance of up to 1.5 km. The kolonok goes up to 50 m under snow without exiting to the surface (Shaposhnikov, 1956). The kolonok rarely gets up into trees. Following water voles, it swims easily and quickly, going out far from shore (Sludskii, 1953).

Seasonal migrations and transgressions. Seasonal migrations (autumn-winter) from one habitat to another are known in the kolonok, as well as migrations for considerable distances related to food insufficiency; however, factual data on these translocations are insufficient since they were often confounded with sharp



Fig. 256. Tracks of a young male kolonok on soft first snow on the ice of a mountain creek. "Kedrovaya Pad'" preserve, southern Primor'e. March 1964. Photograph A.G. Pankrat'ev.

fluctuations in numbers. Data on massive migrations of kolonok in western Siberia and northern Kazakhstan in 1928 are more reliable. The massive transfers were observed in a northern direction, and were associated with reproduction in water voles. In October 1928, migration of kolonok and ermines was observed through the city of Tomsk from west to east. Active broadening of the range of kolonok is associated with years of significant increase in its number as a result of particularly favorable feeding conditions, and may be regarded as a particular type of migration. Seasonal migrations occur in connection with changes in conditions of food capture and their dispersion among habitats.

Reproduction. In the kolonok, the period of rut is quite extended. The timing is subject to geographic variation: in western Siberia, the signs of ruts appear at the beginning of February, continuing through the end of March (Velizhanin, 1931; Zverev, 1931). In Primor'e, rut proceeds from the first third of March and continues to the end of April. In the Pushkin fur sovkhoz near Moscow, rut in six pairs of kolonok took place from 25 April to 15 May (G. Uspenskii, 1933).

Mating lasts up to 35 min. and occurs repeatedly. Timing of pregnancy ranges from 38 to 41 days (Sludskii, 1953), and according to other data—within limits of 35–42 days (Kler, 1941). Parturition was also observed after 28 days subsequent to the last mating, which is considered the minimal period of pregnancy (G. Uspenskii, 1933). The number of young (in caged conditions) ranges from 4 to 10 (7 on average).

Growth, development and molt. Young are born blind and almost naked, with sparse white wool. After some days, they become covered with light yellow wool. Their eyes open on the 28th–30th day. Lactation stops at the end of the second month. By the end of August growth stops, and the young differ from adults only by their darker color, the deciduous tooth formula, and the less massive bones of the skeleton. Also at the end of August, the litter begins to disperse.

Molt occurs twice a year—in spring and autumn.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Sable, both species of ferrets, red fox and eagle owl belong among the enemies of the kolonok. Ferrets, mink, sable, ermine, solongoi and red fox may be competitors of kolonok in the capture of food. Diseases have not been studied, but cases



717 Fig. 257. Tracks of kolonok (left) and otter on snow along a montane creek in a place of typical habitat of kolonok. "Kedrovaya Pad'" preserve, southern Primor'e.

February 1965. Photograph A.G. Pankrat'ev.

of massive mortality of kolonok from unknown reasons are known (Sludskii, 1963).

Parasitic infection of kolonok, according to the data of Sikhote-Alin' preserve (Yu.A. Salmin and V.D. Shamykin), is very considerable. In summer, mites (*Ixodes persulcatus*) cling to them, and late in autumn *Dermacentor canina*. The frontal sinuses of all adult individuals are infected with the nematode *Scriabingulus nasicola*. *Filaria* is encountered in 69.4%, and ascarids in 24.4% (from 10–15 to 30 individuals). Infection with other endoparasites is low.

Fluctuations in numbers of the kolonok are known within the borders of the whole range and are closely associated with the yield of mouse-like rodents or water voles. Usually, years with an increase in numbers of kolonok follow years of massive rodent reproduction. For some regions of western Siberia, increases in numbers of kolonok were recorded in 1910, 1916–1917, 1922–1925 and 1928 (Lavrov, 1937). There is a basis to propose that years of intensive colonization of kolonok beyond the borders of its range coincide with years of increase in its numbers and the very colonization is associated with food deficiency in the regions of reproduction (Lavrov, 1937; Sludskii, 1953).

Field characteristics. Tracks of kolonok on the snow resemble those of ferret, which makes their observation difficult in regions of co-occurrence. Paw prints of kolonok are smaller and more expanded than those of sable. The distance between the paired prints of the paws (length of leap) in an undisturbed running animal is 35 cm; a frightened kolonok makes leaps of up to 1 m. In contrast to ferrets, running of the kolonok has a somewhat confused character, is twisted, and more closely approaches that of mink, ermine and weasel (P.Yu.).

Practical Significance

The kolonok is a valuable fur animal, having a significant share of fur preparation of Siberia and the Far East. The fur of the kolonok is used as both natural and for imitating more valuable species. The guard hairs of the tail are highly valued: used in the preparation of brushes for painting. Settling near villages, the kolonok may cause known harm to poultry, but at the same time, it is useful for destroying rodents. In regions of intensive muskrat raising, the kolonok may also be considered harmful. On the whole, however, the kolonok is undoubtedly a useful and valuable animal. The kolonok is hunted by shooting with dogs, or various box traps, (kulenki, plashki, cherkany) and rarely with jaw traps (P.Yu).

RUSSIAN, OR EUROPEAN, MINK

Mustela (Mustela) lutreola Linnaeus, 1761

1761. Viverra lutreola Linnaeus. Fauna Suecica, p. 5. Finland.1777. Lutra minor. Erxleben. Syst. Regni Anim., 1, p. 451. Renaming of lutreola Linnaeus.

- 1879. Lutreola europaea Homeyer. Zoolog. Garten, 20, p. 184. Renaming of lutreola Linnaeus.
- 1912. Mustela (Lutreola) lutreola wyborgensis Matschie. Sitzungsber. Ges. naturforsch. Freunde Berlin. 1912, p. 347. Vyborg, north of Leningrad.
- 1912. Mustela (Lutreola) lutreola cylipena. Matschie. Ibidem, p. 348. "Gross-Shirau, vicinity of Valau, East Prussia" (between Chernyakhovsk and southeastern corner of Kursk Gulf, Kaliningrad district; V.H.).
- 719 1912. Mustela (Lutreola) lutreola budina. Matschie. Ibidem, p. 349. "Ortelsburg, East Prussia" (Shchitno southeast of Ol'shtyn [Olsztyn], northern Poland; V.H.).
 - 1912. *Mustela* (*Lutreola*) *lutreola varina*. Matschie. Ibidem, p. 351. Vic. of Shverin, Mecklenburg.
 - 1912. *Mustela* (*Lutreola*) *lutreola albica*. Matschie. Ibidem, p. 351. Levitts [Lewitz] river—tributary of the Elbe. Mecklenburg.
 - 1912. Mustela (Mustela) lutreola glogeri. Matschie. Ibidem, p. 354. "Brig [Brzeg], Silesia" (Bzheg, southeast of Vrotslav [Wroclaw], Poland; V.H.).
 - 1932. Mustela lutreola transsylvanica. Ehik. Allat. Közlem, 29, p. 142. "Komitat Turoch, Austro-Hungary" (district south of Beskid, Czechoslovakia—about 150 km southwest of Krakow; V.H.).
 - 1932. Mustela lutreola hungarica; Ehik. Ibidem, p. 142. Kovachna; Transylvania, slightly west of the sources of the Buzeu [Buzäul] River, Romania, Nomen praeoccupatum—Mustela eversmanni hungarica Ehik, 1928.
 - 1939. Mustela (Lutreola) lutreola turovi. Kuznetzov. In: Novikov. European mink, p. 47. Caucasus.
 - 1939. Lutreola lutreola borealis. Novikov. Ibidem, p. 63. Milet village, former Bogorodsk Co. Moscow governance. Nomen praeoccupatum—Mustela flavigula var. borealis Radde, 1862.
 - 1939. Lutreola lutreola caucasica. Novikov. Ibidem, p. 63. Prokhladnaya Station, northern Caucasus. Nomen praeoccupatum—Mustela nivalis caucasicus Barrett-Hamilton, 1900.
 - 1944. "L. (utreola) l. (utreola) turovi Kuznetzov et Novicov." Bobrinski. In Bobrinskii, Kuznetsov, Kuzyakin. Guide to the mammals of USSR, p. 127. In place of Mustela (Mustela) lutreola turovi Kuznetzov, 1939.

- 1951. Mustela lutreola novikovi, Ellerman et Morrison-Scott, Checklist Palaearct. Indian Mammals, p. 263. Renaming of Mustela (Lutreola) lutreola borealis Novikov, 1939.
- 1951. Mustela lutreola binominata. Ellerman et Morrison-Scott. Ibidem. p. 263. Renaming of Lutreola lutreola caucasica Novikov, 1939 (V.H.).

Diagnosis

General coloration monotone and evenly brownish; venter same color as dorsum or a bit lighter. Upper lip, lower lip and chin white in color, sharply demarcated from dark color of head. White spots of various size and form often on chest and along lower neck. Postorbital constriction of skull weak-its width equal to or more than width of interorbital distance. Upper molar relatively small and longitudinal diameter of its inner lobe somewhat larger than outer part of tooth. Dimensions relatively large—the condvlobasal length of male skull more than 55 mm, of female, more than 52 mm (V.H.).

Description

Concerning general appearance, the mink is a typical representative of its genus and has a greatly elongated body with short limbs; however, compared to species described above, it is put together more compactly and does not look so elongated and thin. In this respect, it differs even from the kolonok and stands nearer to ferrets, greatly reminiscent of the black (M. putorius).

Head in mink relatively quite large, with broad, but not tall, ears (in winter, they slightly protrude from fur). Limbs short, relatively well developed membranes between digits, particularly on hind paws. These are larger than in ferrets and only terminal 720 phalanx remains free. Tail relatively short, does not exceed half of body length, constituting about 40% of its length. It is covered by more or less similar, close fitting hairs similar in length throughout, and not fluffy—the same type as other species of genus, strongly differing from fluffy tail of kolonok. Feet below weakly covered with fur. Digital and sole pads visible both in winter and summer; they have light color. Claws light-horn in color.

Winter fur of mink very thick and dense, though not long, and quite loosely fitting. Compared to terrestrial species of the genus, underfur particularly dense. Guard hairs quite coarse, lustrous, and as in all "amphibious" mammals, contour hairs have very wide, flattened middle part. Difference in length and density of fur on various parts of body, in particular on back and belly, relatively very small. These and several other peculiarities of the mink fur are associated with its semi-aquatic way of life.

Summer fur somewhat shorter, coarser and less dense than winter one; however, this difference is small and incomparably less than in other, purely terrestrial, species of the genus³⁵.

Color of winter fur is dark-brownish and of comparatively slight variability. Particularly dark individuals are dark-brown and even almost blackish-brown in color, light ones have reddish-brown color. The tinge of reddish highlights varies, but is usually not great. Color is evenly distributed over the whole body. In only a few cases, ventral surface is a bit lighter than the dorsal side of the



720 Fig. 258. Russian mink, Mustela (Mustela) lutreola L. Sketch by A.N. Komarov.

³⁵Details on fur structure of Russian mink are absent in literature. American mink, acclimatized in our country has been very well studied by our authors. Data on this latter may also characterize the main peculiarities of our mink; however, it is necessary to keep in mind that the American mink possesses in the fur trade higher quality and is more highly valued; its fur is longer and more dense.

body, and in particularly dark individuals and races, a dark, in some even black, broad dorsal belt is noticed. Limbs are slightly darker than trunk, as is tail, the end of which may be almost black. Underfur is bluish-gray. Mink fur, particularly dark individuals, is very beautiful and has a dense silky luster due to dark guard hairs.

Mink has no color pattern at all on the head, and it has a color in common with the whole trunk, but upper and lower lips and chin are pure white. Pattern of upper lip is quite stable, but on chin, varies in size and form. It sometimes occupies the anterior part of the chin, and sometimes extends backward under the entire lower jaw; the posterior border is white, sometimes straight and sometimes uneven.

White markings sometimes occur on the lower surface of the neck and on the chest. They differ greatly in number, form and size. Sometimes, it is one small, hardly noticeable white dot, and sometimes, a sharply defined one, and sometimes several spots; in some mink, there is formed a long narrow white band going from throat to chest, in some cases, the chin spots extend backwards and occupies the throat region; with this there may be a spot or spots on the chest. Finally, and not too rarely, in some places the whole lower surface of the neck and the chest may be white. In this case, the spot is not smaller, and sometimes is greater, than the throat spot of the stone marten. In individuals with a particularly large spot on the chest, white wool covering the digits of the fore- and often also the hind feet, usually occurs.

In mink with very dark fur, "graying" may be present—white ends of individual guard hairs, or some quantity of them spreading throughout the pelage are completely white. Extreme exotypic deviations in the form of albino mink, or pelage covered with separate white spots, may occur.

Color of summer fur differs only slightly from winter. It is usually a somewhat lighter, dirty tone, with a more obvious reddish highlights, with short, dull guard hairs—without dark silky or silvery luster.

On the whole, individual variation in color, if white markings on chest and throat are not considered, is not great. Sexual differences in color and fur character are absent. Young mink are clothed in dull, short and coarse "plump" fur. The first winter coat does not differ from the comparable coat of adults.

Geographic variation is relatively small (see below) and is manifested in lighter and more reddish color of fur from north to south. White markings on throat and chest are quite rare in the north, and are encountered more frequent in a southerly direction; their general area increases and they attain their greatest development in the extreme south of the range (Caucasus). Just here—and relatively often—individuals with the described large white field of "marten" type are observed, which are absent in the north, or are represented there as completely individual rarities.

Compared to the skull of the kolonok, the skull of the mink is on the whole less elongated and with a less elongated braincase, with longer and more widely separated zygomatic arches, and with a relatively less massive and slightly longer facial portion. In several respects, it has characteristics similar to the skull of the black ferret (*M. putorius*). These apply mainly to the relatively general shortening of the skull, width of the zygomatic arches and several other characters. Based on some characteristics, the mink skull occupies an intermediate position between the skull of kolonok and that of the black ferret.

For the rest, the mink skull is characterized by the following characters. It is flattened, with a moderately elongated braincase and almost straight upper profile. Only in the region of the superorbital processes and somewhat behind them, it has a small elevation; the profile of the facial part descends quite steeply anteriorly. The postorbital constriction is weak-its width at the narrowest point is approximately equal to or greater than the interorbital width. The zygomatic arches are relatively weak and are moderately widely separated, the mastoid processes are relatively weakly developed. The auditory bullae are small, swollen, relatively short and narrow, and widely separated; in the posterior part, they separated from each other significantly farther than in the anterior part. The ratio of their length to their width is approximately 1:1.7. Sculpturing of the skull is not sharp, crests and prominences are moderately developed. The occipital crest is well defined, the sagittal one is apparent, but quite weak.

The upper molar is small and weak—its area in projection is considerably less than the carnassial tooth and the longitudinal diameter of the inner lobe is not greater or only slightly greater than the longitudinal diameter of the outer. The posterior end of the second upper premolar is in contact with the anterior outer

edge of the carnassial tooth, but it does not lie in the groove on 723 its anterior edge. The inner surface of the main apex of the lower carnassial tooth is smooth, without a vertical edge.

On the whole, appearance the specializations of the skull, as a carnivore skull, are less developed than in ferrets and even less than in the American mink.

Except for dimensions (see below) the female skull is differentiated by some less developed protuberances, crests, etc. and lower weight, as in all other members of the genus. The juvenile skull is characterized by weaker development of the facial part, its shortness and a more swollen braincase.

Geographic variation of the skull, besides general dimensions, several of which exhibit growth from north to south, is manifested in the fact that in the extreme south (Caucasus) the elevation of the skull in the interorbital region increases (strengthening its similarity to the kolonok) and several features appear (greater constriction of the postorbital region), some of which make the Russian mink approximate to the American (M. vison; see below).

The structure of the os penis is generally typical for the majority of species in genus, i.e. tip of the bone is bent upwards in the form of a hook and even somewhat backward, but the groove on the lower side of the bone is wider than that in the ferret and kolonok and the tip is bent in the form of a spoon (Novikov, 1956). If the bone is viewed from below, the terminal part deviates somewhat to the right.

According to body and skull measurements, the mink belongs to the group of large species of the genus—the ferrets and kolonok. Dimensions of the species as a whole: body length of males is 284–M373–430 mm, of females, 320–M352–400 mm; tail length of males is 124–M153–190 mm, of females, 130–M150–180 mm; length of hind foot of males is 54–M59–64 mm, of females, 50–M52–53 mm; height of ear in males is 20–M23–25 mm. Male tail constitutes 35–M41–52% of body length, of females, 37–M40–45%.

Condylobasal length of male skull is 56.4–M62.7–68 mm, of females, 52.8–M61.4–65.7 mm; interorbital width of males is 11.0–M13.6–15.4 mm, of females, 11.1–M12.4–14.0 mm; zygomatic width of males is 30.8–M35.5–40.0 mm, of females, 28.9–M32.3–37.0 mm; mastoid width of males is 27.0–M31.7–34.9 mm, of females, 26.5–M29.4–31.7 mm (Novikov, 1939).

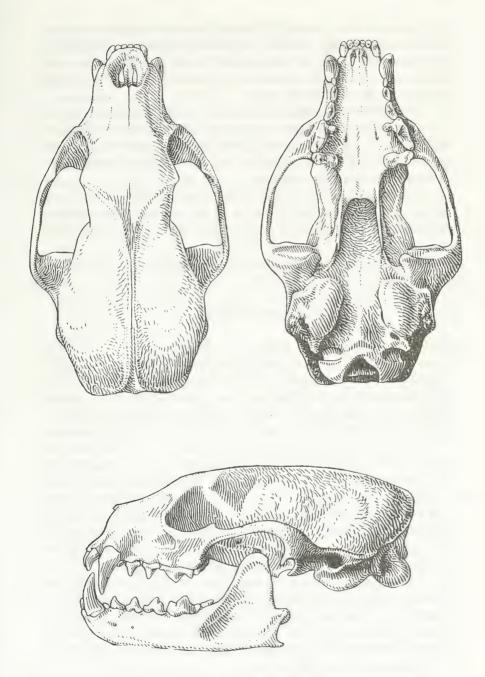


Fig. 259. Skull of Russian mink, Mustela (Mustela) lutreola L.

Dimensions of mink (18) from Volga-Kama Territory: body length of males is 310–M375–406 mm, of females, 300–M327–360 mm; tail length of males is M145 mm,* of females, 120–M128–142 mm; length of hind foot of males is 52–M56.2–61 mm, of females, 45–M50.0–58 mm.

Condylobasal length of male skull is M67.5 \pm 0.40 mm, of females, M63.7 \pm 0.52 mm; zygomatic width of males is M35.2 \pm 0.52 mm, of females, M30.5 \pm 0.65 mm; interorbital width of males is 12.9 \pm 0.30, of females, 11.3 \pm 0.32 (V.A. Popov, 1949; here also other measurements).

Length of os penis of adult males (6) is 34.8-M35.9-37.8 mm, of young, (10) 32.6, M33.5-34.8 mm; its weight in adult males is 0.230-M0.292-0.380 gm, in young, 0.100-M0.118-0.130 gm (V.A. Popov, 1949).

The total weight (from data for Middle Europe) is 550 to 800 gm (V.H.).

Systematic Position³⁶

The systematic position of mink among those species which are here united in the genus *Mustela*, has been evaluated entirely differently by different authors. An extreme point of view holds that the European mink together with the American mink (*M. vison*) belong in a special genus *Lutreola*, usually standing as more or less closely related to the kolonok ("*Kolonocus*") and to polecats ("*Putorius*"), more often to the latter. In such an evaluation of the characteristics of the mink, it is impossible not to see extreme over-estimation, of a known hypothesis of their unique way of life.

724 Right now, this point of view has almost no supporters. More often, both species were included, and are included, in the genus *Mustela* in the category of a separate subgenus, equivalent to ferrets. Isolated opinion holds that minks represent a special subgenus in the genus of polecats (*Putorius*; Stroganov, 1962).

At the same time, in morphological features, mink have no characteristics which should force any higher evaluation of them. According to the sum total of characteristics, the mink itself represents a development and combination of the same set of features which characterize the previously described species of the genus.

^{*}No range given-Sci. Ed.

³⁶For section on American mink, see end of book in "Supplement to the order of carnivores".

Within the limits of the genus, it is most correct to consider it close to the kolonok (*M. sibirica*) on one side, and on the other, already displaying several characteristics of the ferrets, namely the black *M. putorius*. To a certain extent, its position is intermediate, connecting the group of true ferrets ("*Putorius*") with the other members of the genus. Therefore, consideration of ferrets as an independent genus has become practically unsupportable.

The "intermediate" position of mink is emphasized by the fact that in nature hybrids between mink and black ferret are encountered, and these do not represent exceptional rarities. There are such specimens in museums (Z[oological] M[useum of] M[oscow] U[niversity]) and they are described (Ognev, 1931). They are well known to furriers, who even have a special name for them ("khor'-tumak") and affirm that they are met with "not rarely". On the skins of hybrids, characteristics of one or the other parental species predominate (Kuznetsov, 1952). Remarks stating that "data on crosses between mink and ferret are completely absent (Novikov, 1939) is based on misunderstanding. Nothing is known concerning fertility of "khor'-tumak".

Of all species of the genus, the European mink is closest to the American mink (*M. vison*). This latter itself represents a further development of the mink type and compared to it, the European mink carries certain infantile features (larger protuberances, crests, etc. of the skull, development of postorbital constriction in the American mink and some other features—see description of this species).

Despite closeness in their general form, however, they cannot be considered races of one species, as several European authors have done (Zimmermann, 1959; Gaffrey, 1961). The morphological characteristics which divide them are substantial. Hybridization of both species in nature, which is sometimes assumed for Central Europe (Gaffrey, 1961), is not confirmed. On the contrary, in our country a clear antagonistic relationship between the two species in nature, and destruction of one by the other, has been established (V. Popov, 1949, see also section on American mink). Attempts to cross both species in captivity were not successful.

In the sense of the structure and phylogenesis of the genus, it is very interesting that the European and American minks, in their degree of specialization and development of separate concrete characters (postorbital constriction, for example), themselves répresent species parallel to the black (M. putorius) and white (M. eversmanni) ferrets (see also section on American mink) (V.H.).

Geographic Distribution

Europe except the south and northwest Caucasus, western part of western Siberia.

Geographic Range in the Soviet Union

This constitutes the greatest part of the species range—at the present time, nearly the whole. It occupies the European part of the Union, Caucasus and the western part of western Siberia.

The northern border of the range in the extreme northwestin Karelia, passes a little north of the Kem' river—at the southern extremity of Topozera [lake] and Kuzema [city] (Marvin, 1950, 725 1951) or a little to the north (Kesten'ga), but it does not reach Kovdozero, i.e. it generally lies between 65° and 66° N or along 66° N. lat. References to its occurrence near Kandalaksha and even Umba (Ogney, 1931) and, in general, on the Kola Peninsula are mistaken (Pleske, 1886; Novikov, 1939). Farther, the border passes along the shore of the White Sea to Arkhangel'sk, and thence along the sea coast or near it—to the mouth of the Kuloi and Mezen'. From here, the border line, passing south around the Kanin tundra, adjacent to Cheshsk inlet and Malozemel'skaya tundra, passes around Sula (left tributary of lower Pechora) from the north. and along the Pechora, extends as a projection, to the delta, i.e. to 68° N. lat. (Novikov, 1939; V.Ya. Parovshchikov). This is the northernmost point of the range.

Farther to the east, the border includes the entire lower and middle course of the Pechora, skirting the Bolshezemel'skaya tundra from the south along the crooked-forest belt, north around the basin of Usa (apparently, only the lower reaches of its right tributaries, Laya and Kolva), and ascends along its tributary, Ad'zva, to Khased-Khard. To the east of the White Sea, the northern border of the mink range extends, therefore, to the southern part of the forest-tundra or along its southern boundary, moving up the river valleys to the north. Locally, the mink occurs only as a transient (perhaps also living there) at the border of the true tundra (at Nes' village on the western bank of the Kanin, north of the Arctic Circle).

In the Urals, the location of the border is unclear. Apparently, descending from Khased-Khard directly, or almost directly, to the south, it crosses the Urals somewhere around the Arctic Circle or probably south of it³⁷. Farther, the border goes directly south, including the Lyapin river (noted mainly at Saranpaul') and the upper course of Severnaya Sos'va. Thence, in an as yet undetermined path, directs itself, apparently, again southwards and then turns eastwards reaching the Ob' somewhere a little below Tobol'sk. From this point, the range border passes along the Ob' or a little to the north to the lower course of the Agan river, the right tributary of the Ob' (I. Laptey; perhaps transients). Thence, the border line goes directly south, covering the basin of the Dem'yanka (mink is known from several places in its middle course) and reaches Tara on the Irtysh. Beyond the Irtysh, the range does not extend above its course (Yanushevich and Arkhangel'skii, 1952; I. Laptev, 1958).

The southeastern and southern borders of the mink range in western Siberia is poorly known. On the whole, from Tara, it arches to the Ural ranges, somewhere approximately at the latitude of Chelyabinsk. South-southwest of Tara the border, apparently, passes a little north of Petropavlovsk (transient mink are known at Lake Chagly north of Kokchetav; Sludskii, 1953) and at Zverinoglovskaya on the Tobol south of Kurgan (I. Laptev, 1958).

Farther, the border follows along the eastern slopes of the Urals southwards through Orsk to Aktyubinsk, then westwards along the Ilek; it includes the lower course of the Utva (Chingurlau) and reaches the Ural at Ural'sk or slightly to its south. Mink do not occur lower along the Ural [river]. The suggestion (Novikov, 1939) that mink is absent in the southern Urals and inhabits only the western slope in this region, is incorrect (Shvarts, Pavlinin and Danilov, 1951; Kirikov, 1952). Probably transient mink are known at Ilek, on the Irgiz river (Kopa settlements; Sludskii, 1953). Information concerning the occurrence of mink in Alakol'(Semirech'e; Shnitnikov, 1936) are lacking any basis.

From Ural'sk the border, going west, extends over the basin of the Volga tributaries—Bol'shoi Irgiz (Elpat'evskii, Larina and Golikova, 1950; mink are absent on the Uzen') and descending

³⁷The reference that the mink is distributed in the Urals nearly to 70° N. lat. (Shvarts, Pavlinin and Danilov, 1951) was based on some sort of misunderstanding, or it is a misprint; 70° N is the latitude of Vaigach Island.

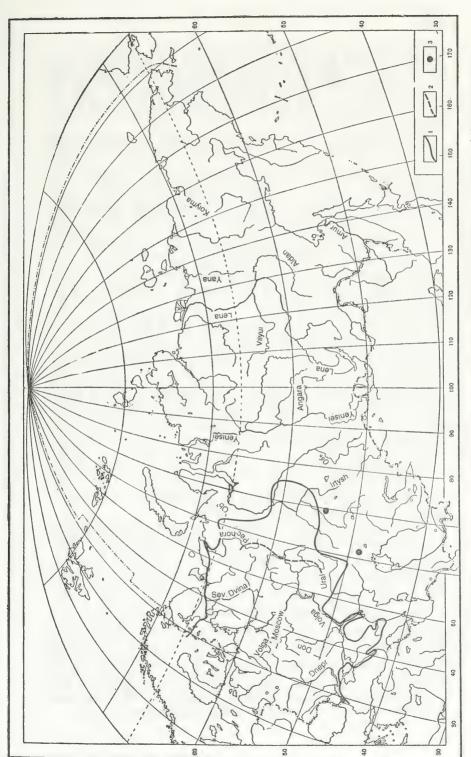
southward, it passes around the basin of the Eruslan from the east (Orlov and Kaizer, 1933), and then reaches the Volga. Along the valley of this river, the range reaches the [Caspian] Sea as a narrow band. Somewhere in the region of maximum proximity of the Volga and the Don, the [range] border crosses over to the Don and descends to its mouth. Thence, it again passes at some distance from the shore along the Azov Sea approximately to Osipenko (Berdyansk) and then, passing around the southern Tavrichesk steppes from the north, reaches the mouth of the Dnepr and along the shore of the Black Sea, passes beyond the frontier of our country.

According to some data (Novikov, 1939), the border envelops the Donets ridge from the north. This is quite possible for the present time, but, apparently, the absence of mink in this region itself constitutes a secondary phenomenon. Equally with this, there are references about occurrence of mink throughout the Ukraine (Migulin, 1927; Korneev, 1952; Sokur, 1960).

In the west, where the range reaches the state frontier, the mink mainly exists in the Trans-Carpathians (Konyukhovich, 1953). The mink is absent in the Crimea.

The outline of the range of mink in the Cis-Caucasus and in the Caucasus is very complicated. The northern border of the Caucasian part of the range begins at the Don at Tsimlyanskaya and descends southward to the Sal, reaching its lower course. Thence, it passes to the Manych, extending along the river eastwards to the mouth of the Egorlyk (Veselovsk reservoir) or somewhat farther, descending along Egorlyk southward and reaching the Kalaus a little above Ipatova. From this point, the border line crosses over the Kuma basin, also including its northernmost tributaries. Along the Kuma, the range border runs to the sea, or somewhat short of it.

The southern border begins at the Caspian Sea somewhat south of Makhachkla (at Deshlagar) and directs itself northward along the foothills, and then westward reaching Khasav'yurt. Thence, along the base of the mountain and along the foothills, it goes to Ordzhonikidze (former Vladikavkas). Farther to the west, it ascends high into the mountains (Beskes, tributary of the Bol'shoi Laba; slightly below Klukhor at the source of the Kuban), it goes in an irregular line through the upper reaches and sources of the Terek, Kuma and Kuban river systems—approximately to the



726 Fig. 260. Distribution of the Russian mink, Mustela (Mustela) lutreola L., in the USSR (V.G. Heptner): 1-border of the present range; 2-eastern border in 1866 (after Novikov, 1939); 3-long transgressions in past decades.

Tuanse meridian. Here, the border crosses the Caucasian range, and the range extends as a narrow strip along the southern slope to the southeast, reaching or almost reaching Sukhumi. Here, the border ascends quite high into the mountains (Pskhu, on the Bzyb' [river]).

In the west, the mink is distributed along the shores of the Black and Azov seas (present in Taman'). In the east, between Deshlagar and the mouth of the Terek, the range is limited to the Caspian shore. In the semidesert, in expanses devoid of rivers between the lower Terek and Kuma (Nogaisk and Karanogaisk steppes), the mink is absent, and the eastern border of the range here goes along the periphery of the Kuma and Terek basins³⁸. As is seen in the description given the range of the mink in the Caucasus, despite the widely propagated view (Novikov, 1939, 1956), is not cut from the main region of occurrence of the species in the European part of the USSR.

In the west, between Karelia and the Black Sea, the range of the mink everywhere goes beyond our state frontier.

There is a widely distributed view that the mink is related to a number of our mammals, the ranges which are expanding to the east. It is usually believed that the above-outlined region of occurrence in the Urals and beyond the Urals, was formed in the last 80–100 years, and in the 18th and first half of the 19th century, mink were absent in Siberia. It did not apparently, occupy the Urals, being met with only on its western side. The mink crossed the Urals, apparently, only in the 70's of the present century and attained the extreme eastern limits of its range only at the beginning of the 30's of our century (by 1932).

It is necessary, however, to keep in view that this opinion about the colonization of mink is based to a considerable degree on information from Sabaneev who is known for his ruinous errors. Generally speaking, little is known on the course of colonization in the mink (for details, see Novikov, 1939; I. Laptev, 1958). That it is continuing to settle new places at the present is not excluded. This is shown by the above-mentioned transgressions of mink to Kokchetav and the Irgiz. Beyond the Irtysh (upper Tara), however, the mink was still absent in 1950 and 1960 (for details, see Novikov, 1939).

³⁸Range in the Caucasus after Dinnik, 1914; Satunin, 1915; Turov, 1926, 1928, 1931; L. Boehm, 1929; Heptner, 1936; Heptner and Formozov, 1941; Vereshchagin, 1947; 1959 and other sources, and after material of V.G. Heptner.

Equally with this, there was a suggestion recently, not lacking in serious foundation, speculating that mink in western Siberia occurred very long ago—even before the academic expedition in the 18th century, but was always rare; and is rare now almost everywhere in Siberia (I. Laptev, 1958). It is possible that, with colonization of mink in western Siberia, there is a situation analogous to that previously mentioned for the pine marten (see p. 844)*.



Fig. 261. Species range of the Russian mink, Mustela (Mustela) lutreola L. In Europe, beyond the borders of the USSR, the range is as established in the 19th—beginning of 20th centuries (after Novikov, 1939, with modifications).

^{*}Page reference omitted in Russian original-Sci. Ed.

On the whole, factual materials supportive of this and other viewpoints are scanty, and the question requires further study.

Information is absent concerning colonization of mink in other directions. Some changes in range are to be expected in connection with the introduction of American mink in many parts of our country.

Geographic Range outside the Soviet Union

This (as established in the 19th and 20th centuries) includes Finland northwards to 66° N. lat. or a little farther, Poland, Hungary, 729 Czechoslovakia, Romania, [eastern]* Austria, Bulgaria north of the Danube and Dobruja**, northern and western Yugoslavia—Istria, Croatia, Bosnia and Herzegovina—i.e. in the west of those countries south to approximately 43° N. lat. and in the east, to Belgrade, the territory of the German Democratic Republic, a considerable part of France (except the southwest and northeast ***). The mink is absent in West Germany, England, Ireland, Denmark, the Scandinavian Peninsula, [western]* Austria, and Switzerland and the remaining part of Europe³⁹.

The mink is rapidly disappearing in the west beyond the boundary of our country and its range is shrinking. It has already disappeared or almost disappeared from Central Europe where it still lived in the beginning of the 20th century. One of the causes of the disappearance of the European mink in western Europe apparently lies chiefly in its destruction by the American [mink] (V.H.).

Geographic Variation

A quite large number of races have been described from the comparatively small species range of the mink, even if we do not

^{*}Russian original ambiguous-Sci. Ed.

^{**}Not clear; Bulgaria lies entirely south of the Danube, and Dobruja is a region of northeastern Bulgaria and adjacent Romania—Sci. Ed.

^{***}In Russian original, "northwest", a lapsus-Sci. Ed.

³⁹Reference to Italy (Bobrinskii, 1944) may apply only to the Istrian Peninsula, now within the boundary of Yugoslavia. In Italy proper, mink is absent and was also absent in the period under review. Data concerning Bulgaria and a portion of Yugoslavia were given by B.M. Petrov. References encountered in the literature concerning the previous presence of mink in the Scandinavian Peninsula and its disappearance not too long ago and its replacement by the American mink (crowding it out or its absorption by hybridization), are incorrect. It was never present there (see Ekman, 1922).

take into consideration the notorious synonyms given by Matschie (1912). In actuality, geographic variation in the species, first of all in the USSR, where the largest part of its range lies, is insignificant and less than is usually reputed to be. This applies both to the amplitude of variation of characters and to the number of races. The relatively small geographic variation in animals associated with water is entirely natural. Usually, six or seven races are recognized, of which there are 5 or 6 in the USSR (Novikov, 1939, 1956; Ellermann and Morrison-Scott, 1951). Such a large quantity partially comes from misunderstanding (Ellerman and Morrison-Scott, 1951, of the Caucasian form, for which two names and two forms are given).

General dimensions, color, density and fluffiness of the fur are subjected to geographic variation. These characteristics change regularly from north to south—dimensions increase, fur lightens, coarsens and becomes less dense. On the whole, both these characteristics, and also in the distribution of the geographic forms of mink, require solid revision.

In our country, it is quite evident that two or three forms can be distinguished. It is possible that several others, highly doubtful forms are still present (chiefly after Novikov, 1939 and Kuznetsov, 1941, 1952 with modifications and additions after materials of the Z[oological] M[useum of] M[oscow] U[niversity]).

1. Northern mink, M. (M.) l. lutreola Linnaeus, 1761 (syn. minor, wyborgensis).

Color dark, brownish-chestnut colored or even dark-brown with diffuse broad belt on back. Tail tip black. Underfur dark, bluishgray. Pelage long, compact and silky.

Body length of adult males is usually 340–M365–380 mm; tail length is 124–M137–150 mm; length of hind foot is 54–M56–58 mm; tail length is 36–42*, averaging 38% of body length. Weight of 100 skins is 6.5 kg.

Condylobasal length of male skull is 56.4–M61.5–64.3 mm, of females, 52.8–M58.2–64.3 mm; interorbital width of males is 11.0–M13.4–15.0 mm, of females, 11.1–M12.8–14.0 mm; zygomatic width of males is 32.4–M34.1–36.9 mm, of females, 28.9–M32.1–37.0 mm; mastoid width of males is 27.0–M29.7–32.2 mm, of females, 26.5–M28.2–31.7 mm.

^{*}In Russian original, mistakenly given as "mm", rather than %-Sci. Ed.

Found in the northern European part of the country southwards approximately to the line Leningrad-Yaroslavl'-Gor'kii-Kazan'-Sverdlovsk; possibly in Bashkiriya.

Outside the USSR-in Finland.

730 2. Middle Russian mink, M. (M.) l. novikovi Ellermann et Morrison-Scott, 1951 (syn. borealis).

Body and skull dimensions moderate—somewhat larger than preceding form.

Color somewhat lighter than in nominal form, dark-tawny or dark-brown, usually with light film of reddish highlights. Dark belt on the back weakly defined or absent. Underfur lighter than in northern mink. Pelage dense and compact, but shorter and less dense, and considerably less silky than in preceding race.

Body length of adult males is 360-420 mm. Weight of 100 skins about 8 kg.

Condylobasal length of male skull is 59.2–M63.7–66.8 mm, of females, 57.2–M58.3–59.4 mm; interorbital width of males is 11.9–M13.8–14.7 mm, of females, 11.3–M12.3–13.9 mm; zygomatic width of males is 30.8–M36.3–38.6 mm, of females, 31.2–M33.0–36.7 mm; mastoid width of males is 28.4–M31.2–33.2 mm, of females, 28.0–M29.2–30.3 mm.

Found in middle zone of European part of Union, south of distribution area of previous form in west, including Estonia, eastern part of Latvia, Byelorussia, southward to border of species, except the Cis-Caucasus and Caucasus, and, probably, eastern Ukraine, Lower Don and Lower Volga regions. The position of mink in Bashkiriya is not clear.

Outside the USSR, probably not encountered.

3. Caucasian mink, M. (M.) l. turovi Kusnetzov [in Novikov]*, 1939 (syn. caucasica, binominata).

Body and skull dimensions large—the largest of the races living within the boundary of the USSR. Skull relatively massive with well developed protuberances, crests, etc. and strong zygomatic arches. Postorbital constriction strongly expressed. Line of upper skull profile in region of supraorbital processes somewhat elevated.

Pelage quite long, but sparse and rough, with less compact underfur. Color light-tawny or light-brown with clear rusty (reddish) highlights. Underfur light, bluish-gray. White markings on chest frequent, and much more often than in other forms; in many

^{*}See note below-Sci. Ed.

cases, large white spot located on chest, sometimes covering entire throat and anterior part of chest. Often, in such mink, ends of limbs also white.

Body length of males usually more than 42 cm. Weight of 100 skins about 9 kg.

Condylobasal length of male skull is 60.8*-M58.2-68.0 mm, of females, 54.0-M56.3-59.4 mm; interorbital width of males is 12.7-M14.0-14.9 mm, of females, 12.0-M12.5-13.2 mm; zygomatic width of males is 34.0-M36.8-40.0 mm, of females, 32.0-M33.3-35.8 mm; mastoid width of males is 29.4-M31.8-34.9 mm, of females, 30.5-M30.8-31.2 mm.

In Caucasus, Lower Volga and Lower Don regions; probably eastern Ukraine.

Absent outside USSR.

Slight elevation of skull in region of supraorbital processes resembles somewhat the corresponding structural peculiarity of kolonok. On the other side, dimensions and relatively massive skull and the more pronounced postorbital constriction combine to make skull of Caucasian mink somewhat similar to American mink skull.

Note. The name turovi, given to Caucasian mink, appeared in literature in 1939 in the work of G.A. Novikov, based on B.A. Kuznetsov's manuscript on page 47. On page 62, G.A. Novikov describes this same Caucasian mink as a special new subspecies under the name caucasica, putting the name turovi of Kuznetsov as its synonym. Later, N.A. Bobrinskii (1944) applied the name "turovi Kuznetzov et Novikov, 1939" to the Caucasian mink. In this draft, the name conformed and was used later (Novikov, 1956). What G.A. Novikov (1939) placed in quotation marks on page 47 was a complete diagnosis from B.A. Kuznetsov's manuscript with his data showing distribution, more precise type locality and occurrence (see above, synonymy of species); the Caucasian form of the mink must be named as given above, but not attributed to G.A. Novikov or to both authors.

Of the three described forms, the most distinguishable is the northern, M. (M.) l. lutreola and the Caucasian, M. (M.) l. turovi. They are well delineated forms differentiated both by their body and skull dimensions, and also fur color and characteristics, and by

^{*}Sic; judging from values of mean and maximum, probably should be 50.8 mm—Sci. Ed.

Nothing is known about the systematic characteristics of the Siberian mink. No differentiation from the described forms should be presumed to have occurred.

4. Middle European mink, M. (M.) l. cylipena Matschie (syn. budina, varina, albica, glogeri, hungarica)⁴⁰.

Dimensions very large, only slightly inferior to Caucasian mink, *M.* (*M.*) *l. turovi*. Color quite dark, apparently, corresponding to color of Middle Russian mink *M.* (*M.*) *l. novikovi*.

Body length of males is 420-430 mm, of females, 370-400 mm; tail length of males is 160 mm, of females, 140-180 mm.

Basal skull length of males is 58.8–M60.6-63.1 mm, of females, 53.3–M54.0-54.9 mm; interorbital width of males is 13.3–M14.2-15.2 mm, of females, 11.8-12.0 mm; zygomatic width of males is 35.5–M37.3-38.4 mm, of females, 32.4-32.6 mm; mastoid width of males is 30.8–M31.9-33.3 mm.

In Kaliningrad district, Lithuania, and western Latvia.

Outside the USSR—in Middle Europe, except the extreme west (France) and, probably, in Hungary, Romania and Yugoslavia: Poland.

A very little known, essentially doubtful form, the characteristics and distribution of which are poorly studied in our country and which cannot be considered established; the same, it can be said emphatically, also applies to Central Europe, where, moreover, the mink is exterminated or almost exterminated at the present time. Establishment of the actual nature and independence of this race is only possible now on the basis of material from our

⁴⁰The name *hungarica* is considered to be a synonym of the form *transsylvanica*. As shown above (see synonymy), it is described from the immediate vicinity of the type locality of the form *gloyeri*, *i.e.* cylipena.

territory. It is not excluded that the Middle European form is very close, and may be identical to, the Middle Russian.

5*. Romanian mink, M. (M.) l. transsylvanica Ehik, 1932.

Dimensions smaller than those of Caucasian form. Color dark-tawny.

Found in Moldavia (?) and Carpathia.41

Outside the USSR—in Rumania, possibly Hungary, Bulgaria and Yugoslavia.

To the highest degree, a poorly known and entirely doubtful form.

Of the described forms having a relationship to our fauna, only two or three (nominal, Caucasian and Middle Russian) may actually be considered real; the remainder are very doubtful and basic study is required of geographic variation of the species in the Pribaltik, the western parts of the Ukraine, Poland and Middle and southeastern Europe.

* * *

Outside the borders of USSR, still another form is usually recognized, M. (M.) l. biedermanni Matschie, 1912—France (V.H.).

Biology

Population. The distribution of the mink within its range has the character of a fine lacey network, since its innate area is restricted to a narrow ribbon along the banks of its preferred small bodies of water. Therefore, density of settlement in different regions depends on frequency of water bodies within the area and the degree of their suitability for the species. On the latter is dependent the density of mink within the home range.

Mink populations and distribution are difficult to determine. Although forests are not absolutely necessary for its occurrence, they nevertheless create the most favorable conditions. Therefore, the majority of mink inhabits the forest zone, and a very small number inhabits the forest-steppe, and even fewer, the steppe zones. Thus, in the northern zone of the European part of the

^{*6} in Russian original-Sci. ed.

⁴¹According to some data (Konyukhovich, 1953), the mink, which is quite widely distributed in Carpathia (Zakarpatsk district), is relatively large and dark and differs from the Middle Russian form. It is now impossible to decide from these data whether it is the given form or the Middle European cylipena.

country, 24% of mink were captured, in Arkhangel'sk and Vologod districts and in Komi ASSR—25%, in the Volga area, Bashkiriya and Urals—23%, and in Kareliya and Leningrad district—15%.

If, in the recent past, the number of Russian mink skins taken annually was equal to 50,000–60,000 (V. Popov, 1964), then at the beginning of the 60's, it became two—three times less. The causes of this decrease are several: a general decrease in intensity of the trapping industry, its crowding out from a series of areas by the American mink, local reduction in numbers due to increasingly unfavorable living conditions etc. The replacement of natural mink fur by cage-bred American mink in the world fur market played a known role. At the present time (mid-60's), judging by the catch, the highest populations of mink are found in Kostromsk, Yaroslav, Kirov, Gor'kii and Arkhangel'sk districts (about 25% of total catch in USSR); i.e., mainly in the southern taiga zone.

Habitat. Most typical for mink are small bodies of fresh running water. It is rarely encountered on large rivers; mainly in flowing valley lakes and at mouths of tributaries. The riparian zone of large and moderate rivers are considerably inferior to the small creeks with woody banks as regards food abundance and the protective conditions. Nevertheless, mink are met with on such rivers as the Volga, Kama, and Vyatka (V. Popov). Mink has not mastered the water surface—it is an inhabitant of the riparian zone.

The dimensions and depth of the water in the summer period do not have primary significance for the mink. Only in the region of the brood den is a depth of not less than 0.5 m necessary for masking the underwater entrance.

In winter period, the presence and abundance of unfrozen sections—polynyas, broken ice, springs—are very important places. No less important is freezing of the water at a high level, with formation then, when it recedes, of a considerable space below the ice. Total freezing of the water is very unfavorable, but when winter food is abundant or when accumulations of hibernating frogs are available, winter survival is not inhibited.

Water bodies where "naled" are formed [water on top of ice surface] are unsuitable for mink. With incomplete freezing, mink feel themself in excellent conditions in winter in very small bodies of water—1.0-1.5 m wide and not more than 1 m deep. In one place, mink prefer steep banks and in another low, marshy ones. The security of riparian zone and channels—litter, availability of

tree and shrub vegetation or bogs with timber along the bank are entirely essential for the well-being of this animal.

Water bodies colonized by mink are extremely variable as regards feed conditions, denning and protection. All of the variation of water bodies as denning areas, may be grouped into seven types: 1) small water bodies with semiaquatic vegetation and low, marshy banks; 2) small water bodies of the meadow type with low marshy banks bordered with willow herb and speckled alder; 3) small meadow water bodies with steep banks, with an interrupted border of speckled alder; 4) small water bodies in coniferous and mixed forests; 5) small water bodies with water meadow of the broad-leaf type; 6) black alder swamps; 7) montane-taiga creeks and rivulets with rapid current and rocky channels. Mink often settle at mill dams, in flood lakes, tributaries and dry river beds, sometimes also in floodlands of large rivers. Winter regimes of water bodies most sharply restrict the distribution of mink.

Food. In composition the food of mink includes almost all elements of the aquatic and riparian fauna. Its food varies depending on composition of this fauna, time of the year, crops of different foods and changing conditions of their availability.

The foods of European mink are poorly studied. Voles are the most significant (36% of occurrences), fish (28.8%), crustaceans (26.7%), frogs (17%) and water insects (19.8%). In Tatariya (floodlands of the Kama), fish is the most important (35%), while mammals, (29.5%), amphibians (18.1%), birds (4.5%) and insects (3.4%) are less so. There are no essential differences between its food and that of American mink (Grigor'ev and Teplov, 1939).

In individual cases, mink is capable of overtaking and catching any fish weighing up to 1-1.2~kg, but it usually prefers smaller ones. Often but not everywhere, mink feed on crustaceans. They are absent not only in the Trans-Urals but also in many water bodies in the European parts of the Union.

The daily food requirement of the mink food consists of 140–180 gm. When food is abundant, mink makes stores. Usually, they are not great and contain, for example, up to 20 loaches [Miagurnus], 3 large ide and pike or several water voles. Sometimes, the store consists of frogs alone. When there are outbreaks of fish kills, the store of mink increases to 10–15 kg (V. Popov, 1941).

Local fluctuations in the abundance and conditions of capture of different foods always occur everywhere, and these are reflected

in mink nutrition. Thus, for example, in Tatariya (Grigor'ev et al., 1931) in the winter of 1929/30 the frequency of occurrence of water voles was twice that of the preceding year (14.2 and 33.3%). On the other hand, the frequency of occurrence of frogs in its food decreased more than two times (11.1 and 27.7%), of fish—by almost 2.5 times (27.7 and 67.8%), and birds completely disappeared from its ration. This is explained by the fact that water voles were plentiful and this food is more calorific than fish and frogs.

Home range. The range inhabited by individual animals is not large, possibly thanks to the generally high food resources on the banks of small water bodies. The dimensions of individual home ranges fluctuate depending on feed resources of a given region. In regions of water meadows with little food, the home range attains 60–100 ha, but significantly more often, the mink lives in an area from 12–14, and up to 27 ha. In summer, the range is smaller than in winter. Along the shoreline, the length of the home range fluctuates from 250 to 2000 m, with a width of 50–60 up to 100 m.

The length of daily movements of mink differs. In spring, individual wandering males move from 4-5 up to 7 km per day. In autumn—from 50 to 1000 m, sometimes the whole movement is situated within the boundary of a water meadow not more than 100 m long (L.G. Kaplanov). In winter, its movement on the snow surface decreases to 100-150 m per day. In the Moscow district in the 30's with very intensive commercial harvest the catch of mink per 1000 ha of denning area consisted of 50 to 200 individuals (P.B. Yurgenson).

Burrows and shelters. Mink has both permanent burrows, as well as repeatedly visited temporary shelters. The burrow is used throughout the year, with the exception of the period of the spring freshets and summer floods. Usually, the burrow is located not more than 6-10 m from the water's edge. It is of simple construction: 1-2 passages 8-10 cm in diameter and 1.40-1.50 m in length, leading to a nest chamber of dimensions approximating 48 × 55 cm (Flerov, 1926). In the brood burrows, this chamber is usually lined with dry grass, moss, mouse wool or bird feathers; sometimes, a lining does not occur at all.

Often, the burrow opens to the outside under water, as in the river beaver, otter and desman. Such underwater outlets are constructed when the bank of the water body, though not high, is abrupt and steep. In other cases, the burrow is made under the

roots of trees, while in marshy places, the burrow is made in high hummocks—"kobla" of European alder or spruce. Often, mink settle in the hollows of riparian trees on the banks or in hollows in the wind-felled branches and fallen trees. Sometimes, it constructs a nest in heaps of reeds, brushwood or under the protection of overhanging sod and woody roots of a steeply rising bank. Near the burrow entrance, a "latrine" sometimes occurs and often food remains are scattered here.

The temporary shelters occur under overhanging banks, in mill pond dams, under haystacks, etc.

Daily activity and behavior. In the summer-autumn period, mink is active throughout the whole 24-hour period without a clear rhythm of daily activity. It more often hunts at dawn and at night. It is especially active in cloudy autumn weather with light rain. In winter, especially in severe frosts, it is less active. With availability of empty spaces under the snow, it does not come out from under the snow surface for many days. Activity of mink noticeably increases in autumn, when the young animals disperse, and sometimes, during the transition from completely frozen bodies of water to those conditions more favorable, and in spring during the breeding season.

The greater part of the time, mink go about on the shores of water bodies. Except for hours of rest, it finds itself in continuous movement in search of food. All its movements are quick and bustling. In case of danger, it tries to hide itself in water, in extreme cases, it conceals itself under roots or fallen trees. It swims and dives superbly. It was shown that it is able to run along the bottom of the water. While swimming, nearly half of its trunk appears above water. In hiding from enemies, it submerges under water leaving only the tip of its nose on the water surface.

Diving, the mink is able to remain under water for 1-2 minutes, swimming in this time 10-20 m. After this, it appears on the water surface for 2-3 seconds and dives again. The mink climbs poorly, but in pursuit, it can climb a tree up to a height of four m. It hides well and observations of it rarely present themselves.

The mink is an animal in which sedentariness is well developed. Due to this, within separate bodies of water, it is very easily killed out. It slowly resettles emptied places.

Seasonal migrations and transgressions. Lengthy migrations by mink have not been noted. In autumn, movements of separate

individual are observed in connection with the changes in food resources of areas and the freezing to the bottom of small forest water bodies. In connection with the dispersion of the young, limited wandering is observed. During these, mink pass from one river or rivulet to another, traversing forest watersheds which extend for several kilometers.

In spring, male mink perform a quite long travels in search of females. At that time, paths of minks are observed along the banks of rivers of Moscow district (P.B. Yurgenson).

735 Reproduction. In Moscow Zoo, estrus was observed on 22–26 April⁴¹.

Mating lasts from 15 minutes to 1 hour and proceeds several times in one day.

Duration of pregnancy has been determined as 42–46 days. Parturition was recorded on 6 June. The number of young in the litter ranges from 3 to 7.

Growth, development and molt. Weight of the newborn European mink equals 6.5 gm. The young grow rapidly, and after 10 days birth weight has trebled. Milk incisors appear quickly. They are born blind and the eyes open on the 30th–31st day.

The lactation period lasts 2–2.5 months⁴², but at the age of 20–25 days, the young already begin to taste food brought by the mother. Coming out of the burrow is noted from 4 to 27 July. On the hunt, they go out with the mother at the age of 56–70 days, and at the age of 70–84 days, they become independent. They attain half the size of adult animals by the end of July, but separate individual of late litters, the size of a rat in August, occur. Mink attain sexual maturity in the following year. Duration of life is undetermined.

As in other aquatic mammals, molt in mink proceeds slowly and gradually, and therefore is unnoticeable.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The otter is the most dangerous enemy and competitor of mink. This is greatly weakened by the known degree to which the otter avoids littered waters and those overgrown with aquatic plants. The otter crowds out the weaker mink from its own home range. Those places where the number of otters increases the

⁴¹i.e., approximately one month later than in the American mink. It is supposed (Rubetskaya et al., 1933) that this is one of the reasons for lack of success in attempts at interspecific hybridization.

 $^{^{42}}$ Milk composition: fat—3.8%, protein—6.2%, sugar—5.6%, mineral salts—10.66%.

number of mink is greatly reduced. A series of cases of direct destruction of mink by otter are known. Inimical competitive interrelationships exist between both mink species. In areas where they live together, the larger and stronger American mink replaces and often destroys the European mink. Competition also occurs with the forest polecat in those cases where it lives in the floodlands of creeks. A case is known of a polecat set upon a mink and dragged it to its burrow (Formozov, 1923).

Diseases of minks in nature have not been studied. Invasiveness with helminth worms was determined as 56% (M.P. Lyubimov). Among helminths, 27 species were recorded in minks: trematodes— 14, cestodes—2, and nematodes—11 (Petrov, 1941). Particularly often, pulmonary filariasis and krenzomatiasis are encountered, as well as skryabingulosis infecting the frontal sinuses. They sometimes die in fishing tackle.



735 Fig. 262. Paired prints of paws and schematic of mink jumping on snow. The legs are usually placed closely in series without skids, in contrast to ferrets and marbled polecat in which the pair of limbs of one side are for ahead. Neya river, Ponazyrevsk region, Kostromsk district. 22 October 1939. Sketch by A.N. Formozov, about 2/3 natural size.

Mink populations independently of the influence of those harvested do not remain at one level. However, a marked sequence in its variation has not been established. Usually, populations grow for 3–5 years. Such widespread death of mink is scarcely connected only with changes in abundance of food. Probably, climatic peculiarities determining the ice regime of water bodies are of greater significance. In the severe winter of 1939/40, when all bodies of water in Karelia were strongly frozen, the number of open-water areas was greatly decreased at the same time that mouse-like rodents were extremely few—resulting in the majority of mink dying from hunger (Sludskii, 1953).

Field characteristics. Tracks of mink are nearly as large as those of the forest polecat, but prints of the pads are larger and more rounded, and the claws are shorter. Distance between the paws are wider than in the polecat, and track in the snow often appear dirty. The gait itself of the mink bears the stamp of restlessness and incessant roving from side to side. In the polecat, the gait is more stable and firm. In winter, the tracks of mink often sink deeply into the snow or are concentrated around open water and shoal areas. In rare cases only does it move away from water for more than 50–100 m (P.Yu.).

Practical Significance

The European mink is a valuable fur animal. During the period of most intensive trapping, the catch in the USSR reaches 50–75 thousand skins. At the present time, catch is regulated by issued licenses.

The most effective means of capture is that utilizing dogs (laika or other breeds). Mink are also successfully caught with jaw traps and box trap types, cage and plashka* and by obmet nets. During the hunting season, the experienced hunter catches 30–40 and up to 100 individuals. Spring harvest with the help of dogs is very damaging in that period when the rising water fills all the empty places under the ice and drives the mink to dry land. Spring hunting is not permitted (P.Yu.).

^{*}Local word for trap/lnet type-Sci. Ed.

Subgenus of Polecats

Subgenus Putorius Cuvier*, 1817

FOREST, OR BLACK, POLECAT⁴⁴

Mustela (Putorius) putorius Linnaeus, 1758

- 1758. *Mustela putorius* Linnaeus. Syst. Nat. Ed. X, 1, p. 46. Upsala, Sweden.
- 1758. Mustela furo. Linnaeus. Syst. Nat. Ed. X, 1, p. 46. Africa, Morocco.
- 1827. Putorius vulgaris. Griffith, Cuvier's Animal Kingd., 5, p. 120. Substitute for putorius Linnaeus.
- 1843. Putorius foetidus Gray. List Spec. Mamm. Brit. Mus. Substitute for putorius Linnaeus.
- 1851. Putorius verus. Brandt. In: Semashko. Russian Fauna, 2, p. 357. Substitute for Mustela putorius Linnaeus.
- 1926. Putorius putorius stantschinskii. Melander. Nauch. izvest. Smolensk. gos. univers., p. 137. Roslavl'sk co., Smolensk gov. Described as a color "variety".
- 737 1929. Putorius putorius orientalis. Brauner. Ukrainsk. mislivets ta. Ribalka, No. 2–3, p. 9, Ukraina. Exact type locality not indicated, but apparently, northern part of former Khersonsk gov. Nom. praeocc.—Mustela erminea orientalis Ognev, 1928.
 - 1932. Mustela putorius rothschildi. Pocock. Scot. Nat. Edinb. Dobrudza River, Romania.
 - 1948. Putorius putorius L. f. piriformis. Kostron. Prace Mor.-slez. Akad. prir. ved., 20, p. 52. Czechoslovakia.
 - 1952. Putorius putorius ognevi. Kratochvil. Sborn. Vysoke skoly zemed. a lesnecke v Brne, No. 1, p. 8. Middle European part of USSR. Nomen praeoccupatum—Mustela erminea ognevi Jurgenson.
 - 1955. Putorius putorius orientalis. Polushina. Ekologiya, rasprostr., i nar.-khozyaistvenn. znachenie sem. kun'ikh zap.-oblastei Ukrainsk SSR, p. 6. Eastward of line Pskov-Minsk-Zhitomir-

^{*}In Russian original, misspelled Guvier-Sci. Ed.

⁴⁴Also known as common polecat (in books). By furriers—black polecat.

Vinnitsa. Nomen praeoccupatum—Mustela erminea orientalis Ognev, 1928; Putorius putorius orientalis Brauner, 1929.

1965. Mustela (Putorius) putorius mosquensis. Heptner. Zool. Anz., 176, H.1, p. 2. Savvino 20 km east of Moscow (V.H.).

Diagnosis

General color brownish-black with light yellowish underfur visible. Lower side of body entirely blackish, without light underfur; large yellow field absent on belly. Tail black throughout whole length. Postorbital constriction weak, its width in narrowest place not less or hardly less than interorbital constriction (V.H.).

Description

The general appearance, habits, etc. of the black polecat are typical of other species of the genus. It also moves mainly in leaps, arching its back high upward, or, slinking down, it creeps. However, it generally has a more compact conformation and, although short-legged, its body is not so elongated as compared even to the mink and steppe polecat. This partially depends, apparently, on strong elongation of the projecting axis, mainly in the posterior part of the back. The tail is relatively short (about one-third of body length), covered its whole length by hairs of approximately the same length and slightly fluffy.

Winter fur quite long, fluffy and soft, although not particularly close-fitting. Guard hairs along back elastic and coarse. Guard hairs particularly long on rump (in the sacral region); anteriorly, they become shorter, and shortest on withers. Fur on belly short, close-fitting. Average number of hairs per 1 cm² on back 8,500–9,000; ratio, one guard hair to 19–20 underhairs, and on abdomen average number of hairs per 1 cm² about 6,000. Length of guide hairs on back about 50 mm, and thickness about 117 mk*; guard hair, correspondingly, 43 mm and 112 mk; and underhairs 26 mm and 20 mk (Tserevitinov, 1958). Winter fur of polecat is characterized by very great difference between length of guard hairs and of underhairs, which is not characteristic for the majority of species in the genus (except steppe polecat), and this causes guard

^{*}Microns.

hairs to appear to protrude above underhairs. This is further accentuated by the contrast in color of the dark guard hairs and the light underhairs (see below). The tail at base is covered by guard hairs about 35 mm in length and with underhairs of about 18 mm. Elsewhere on the tail, guard hairs are about 45 mm.

Anal glands, giving a sharp "polecat" odor, are well developed (polecat may even project their secretion) and serve as a means of defence. There are 3 to 5 pairs of teats, more often 4.

General color tone of adult polecat in winter fur is quite intensive brownish-black or blackish-brown, which is determined by color of long guard hairs. Equally with this on dorsum and sides of body, the dark tone is brightened by bright whitish-yellowish, sometimes yellowish-grayish underfur showing through. What is perceived as bicoloration is obtained by what seems to be a two-layered color of the fur. The light undercoat is not seen equally in different parts of the body. On the back, especially the posterior half, long and numerous guard hairs completely or almost completely hide the underhairs, and the light tone here is not noticeable or lightening is slight. On the sides, it [lightening] is well defined and their general color is strongly differentiated from the general tone of the [dark] spine. Approximately the same relation occurs on the neck. The nape and the shoulder region are darker in color.



Fig. 263. Black, or forest polecat, Mustela (Putorius) putorius L. Sketch by A.N. Komarov.

Throat, lower neck, chest, belly and inguinal region are devoid of light underfur—black or blackish-brown throughout the entire extent. Sometimes, large blackish-brown fields are situated on the chest and inguinal regions and the belly is distinguished by its somewhat lighter, light-brownish tone. The chest and inguinal spots in this case are united along the mid-line of the belly as a narrow black band. Ventral coloration characteristic of steppe polecat is, however, never observed (see [below]). Limbs are pure black or with brownish tint, the tail is black or brownish-black throughout its whole length. Light underfur is absent on the limbs and tail.

A contrasting pattern occurs on the head—the area around the eyes, region between the eyes (anterior part of forehead) and longitudinal stripe along the top of the nose are black-brown—the upper half of the forehead and the whole region between the eyes and ears, cheeks, around the mouth and chin are whitish or white, with a silvery tint on the forehead. Therefore, on the light head there is a "mask" covering the region of the eyes and the area between them. The ears are dark-brown edged with white. Vibrissae are black. Hairs covering the lower side of feet are brownish-black or dark-brown; the digital and footpad callosities are completely covered by them.

The general tone of the fur is variables, occurring from darker to lighter. This mainly depends on the density of the guard hairs which cover, to a greater or lesser degree, the light undercoat and on the intensity of their black tone. Apparently, color is, to a certain degree, associated with age—the older the animal, the redder the color tone of guard hairs and the lighter the general tone of the fur. The color of adult females shows no essential differences, but, apparently, their underfur does not carry rusty highlights and is on the whole whiter and paler.

The summer fur is sparse and coarse, shorter than winter fur (guard hairs not longer than 30-35 mm), grayer, dull and lacking the beautiful luster characteristic of winter fur. Underfur is more weakly developed both in length and density and has a brownishgray or rusty-gray color.

Newborns are almost bare, but in the first days they become covered with short, fine and delicate, but dense, white hairs and they look whitish or almost white. This, apparently, is the delayed development of embryonic pelage (lanugo). At the age of 10 days, this pelage begins to be replaced by the second—the juvenile. Its

fur is short and sparse, but fluffy and soft, quite even over the whole body; guard hairs are not distinguishable ("down-like"). General tone of fur is grayish-tawny-brown with grayish-rusty underfur showing weakly on the sides. Lips and chin are white, but the facial pattern is very variable—in some individuals, the head is uniformly dark, the same color as the trunk, and in others, a quite wide whitish band is located across the head between the eyes and ears. Animals found in the nest are in this fur, and have it in the first days after leaving the nest.

This pelage is converted in the first summer into the pelage of subadult animals. The fur is still somewhat "down-like", but guard hairs are well differentiated from underfur, the head pattern is well defined, and contrast between color of underfur and that of guard hairs is clear. In general variation in color in this pelage is very great. It passes into the first winter pelage which does not essentially differ from the corresponding adult pelage (Herter, 1959,* Kratochvil, 1962 with modifications).

Among exotypic variations of polecat are known complete albinos and in some places, the chromic deviation known as "braginskii polecat" to furriers, and described as "P. p. stantschinskii," is not uncommon. These chromists vary quite greatly in color details. In typical individuals, underfur is usually reddish, brighter than in normal polecats. Guard hairs on the whole trunk are bright and lustrous, reddish or brownish-red, or intensely red. The tail is reddish or reddish-brown. Black guard hairs are not everywhere, being absent on the lower body and head. The venter is light, having the undercoat color and only a large chest spot; inguinal region and posterior part of abdomen are reddish-brown. In extreme cases, guard hairs are so light that in tone, they are only slightly differentiated from the pale-yellow underfur or almost indistinguishable. In this case, the whole animal is very light palegolden-yellow color, with only a small darkening on the chest where a large spot of light-tawny color is [normally] located. Equally with the very bright reddish polecats, animals are found with normally colored underfur and only with reddish guard hairs. They themselves represent a sort of transition between normal individuals and chromists.

Geographic variation in color is weak.

^{*}Not in Lit. Cit.-Sci. Ed.

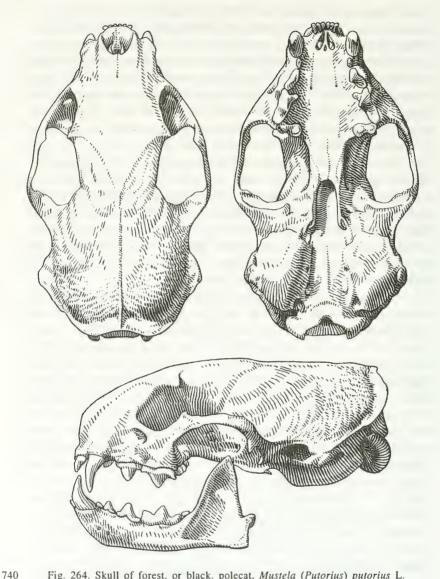


Fig. 264. Skull of forest, or black, polecat, Mustela (Putorius) putorius L.

Skull relatively coarse and massive—more massive and heavier than in mink. It is comparatively short and broad, with a strong but short, broad facial portion. Skull width in region of mastoid processes more than half condylobasal length. Protuberances and crests well developed; occipital crest large, and in adult and old

animals, sagittal crest well defined throughout whole length—as well as anterior branches. Mastoid processes well developed. Zygomatic arches strong, but not widely separated—zygomatic width approximately equal to mastoid or only slightly exceeds it.

Region between supraorbital processes is convex. Line of upper skull profile in facial portion descends anteriorly as a convex arch, and the line of the braincase of skull gradually and slightly descends posteriorly. On the whole, skull somewhat flattened. Supraorbital processes small and protrude slightly laterally. Interzygomatic region of braincase relatively short and broad. Lateral outlines of postorbital portion form almost parallel or only very slightly diverging lines; narrowest place of postorbital portion not in form of sharp constriction—its width here equals to or only slightly less than interorbital width. Greatest constriction of postorbital region with jaws closed usually lies posterior to line uniting apices of coronoid processes of mandibles.⁴⁵

Nasal opening is somewhat compressed laterally and width usually less than height. Auditory bullae somewhat swollen in posterior half; carotid foramen on inner side of bulla lies nearer its anterior end than its posterior. Ends of pterygoid processes have hook-like form and are strongly turned outward. Nasal bones widened anteriorly and posteriorly constricted, forming acute wedge passing between anterior portions of frontal bones. Therefore, upper part of premaxilla comes into close contact with nasal, but not throughout whole length of latter (noticeable only in skulls of young animals).

By comparison with previously examined species in genus, teeth very strong, large and massive in relation to general skull dimensions. Carnassial teeth relatively large, upper molars, on contrary, with smaller dimensions. In large individuals, all described characteristics of skull more strongly developed and defined than in small; the latter reveal certain arbitrary infantile features (see below).

Sexual dimorphism in the skull, not to speak of dimensions, is quite significant. Female skull lighter with less developed protuberances, crests, etc., not so wide and angular, and more narrowly separated zygomatic arches. Supraorbital processes usually smaller,

⁴⁵According to Stroganov (1962), this is one of the most constant features differentiating it from the skull of steppe polecat. Judging by material in Z[oological] M[useum of] M[oscow] U[niversity], it has no such significance.

nasal openings narrower, convexity of skull in interorbital region less, teeth weaker.

In young animals (less than one year), cranial region of skull relatively much larger, convex and does not bear crests; supraorbital processes weakly developed, postorbital constriction weakly defined and narrowest place in this part of braincase lies almost directly behind supraorbital processes. Facial portion of skull and nasal region very short, auditory bullae relatively small; sometimes interparietal bone noted. All these features are more pronounced in younger animals. However, course of age changes in the polecat skull is quite great and comparatively prolonged. One-year-old animals greatly differ from older ones, and the two-year-old animals are well distinguished.

Geographic differences in skull are not manifested.

The os penis, in general features, has a form typical of other species of the genus. Its base is somewhat compressed laterally, tip of bone is bent upward in form of a hook and somewhat twisted to the left. Ventrally, it bears a quite deep groove, continuing on upwardly bent tip. Left side of groove wall slightly elevated and forms a rounded protruding bony flange on very end of hook (Ognev, 1931).

Caecum not developed. Length of male intestine averages about 235 cm, of females about 186.5 cm, weight of male heart averages 7 gm, that of females 4.75 gm (Middle Europe; Herter, 1959).*

Dimensions of the black polecat are subjected to very great variation, on the whole greater than in the previously described species of the genus. This is explained by the considerable difference in dimensions of males and females, and the comparatively slow maturation of the young. They attain complete growth, apparently, only in the third year of life. Equally with this, is magnitude of individual variation in both males, and also females—but especially the former. Besides these "normal" fluctuations in variation, both relatively very small and very large individuals (three types according to measurements already mentioned by Hensel, 1881) are met with among polecats. Measurements of the latter ("giants") are considerably larger than those of polecats of the "normal" type, and lie beyond the limits of usual amplitude of their variation, although connected with them, representing rare positive variants.

^{*}Not in Lit. Cit.-Sci. Ed.

The same applies to very small individuals. The forms of these three types are also known in several other species of the genus, though in the one described here, they occur more often (see also section on steppe polecat). In some cases the possibility of hybrid heterosis (with mink) cannot be excluded; however, this has not been remarked on for "giants."

Body length of males is 350-460 (up to 480?) mm, of females, 290-394 mm; tail length of males is 115-167 mm, of females, 84-150 mm; length of hind foot of males is 42-63 mm, of females, 33-58 mm; ear length of males is 21-36 mm, of females, 15-26 mm.⁴⁷

Condylobasal length of skull of males is 59–71.2 mm (65.2), of females, 51–62.9 mm (55.7); zygomatic width of males is 35–42 mm (34.4); interorbital width of males is 15.8–20.3 mm (17.5), of females, 12.6–18.1 mm (14.0); postorbital constriction of males is 14.3–18.0 mm (16.1), of females, 12.6–15.8 mm (14.3).

Length of adult os penis (8) is 33.5-M36.5-38.2 mm, of young (17), 31.0-M34.0-37.0 mm; weight of penis bone is 0.280-M0.337-0.470 gm, of young, 0.080-M0.146-0.240 gm (Popov, 1949).

There are no reliable data on weight of our polecats (clear errors are sometimes found in literature, for example Stroganov, 1962). Weight of adult males from Middle Europe are 1,000–1,500 gm, females, 650–815 gm (Herter, 1959) (V.H.).

Systematic Position

The steppe polecat, M. (P.) eversmanni is the closest form to the black polecat. Their closeness is undoubted and is generally so great that a series of authors, beginning with Pocock (1936) include them in one species. However, there is insufficient basis or principle for this and, evaluating all their particularities and all sides of their existence, it is more correct to consider both polecats as a closely related, but independent, species (for details, with

⁴⁶The above described extremely wide variation in weasels of the European part of the USSR itself represents a phenomenon whose nature is of a different kind.

⁴⁷After Ognev (1931), Heptner and others (1950), Polushina (1956) and Stroganov (1962) with some additions and corrections, from materials in Z[oological] M[useum of] M[oscow] U[niversity] and others. With skull measurements, average size of Middle Russian polecats after unpublished data of L.G. Morozova-Turova (40 adult males, 24 females) are given in parentheses.

analysis, see systematic position of white* polecat below). From this, the black polecat must, apparently, be considered a less specialized form with several features of an infantile character. In skull structure, adaptation to a predatory mode of life, in particular to capture of larger animals, did not reach the high level of the steppe polecat.

The relationship between the black polecat and mink is sufficiently close, although at a lesser level. The European mink itself represents, in a certain sense, a connecting link between polecats and the remaining species of the genus (for details see the sections on "Systematic Position" of European and American minks). This offers no difficulty, as already mentioned, except for the rarity of hybrids of both species in nature. In recent times, the suggestion was even made (Stroganov, 1962) to include minks in the genus of polecats (*Putorius*) as a separate subgenus.

743

In West and Central Europe, a kind of domestic animal for the destruction of rats in houses and for hunting rabbits is kept, which is called the white polecat, *Mustela furo.*** This form is a typical polecat in its general appearance but is pure white in color with red eyes (albino). The origin of, and systematic relationship between the white polecat and the European as well as black and steppe polecats has been studied frequently, but this question has not been resolved. Some consider it a domesticated albino form of *M. putorius* and others—of *M. eversmanni*. It is also suggested that the white polecat is a special North African form of the black polecat which has been preserved only in a domestic condition. In the majority of cases, this form is recognized simply as "*M. furo*" or "*P. furo*" (for details, see Herter, 1959). White polecats are, apparently, unrestrictedly fertile in crosses with both the forest and steppe polecats.

The skull of "M. furo" is generally typical of the forest polecat; however, in several cases, it bears features characteristic of the steppe (constriction of postorbital region). It has been noted that hybrids of black polecats and "M. furo" closely resemble the Siberian polecat in color (color of lower body).

Apparently, it is more correct to consider that "M. furo" is a domestic form of M. putorius. This is indicated not only by its

^{*}Alternate name for steppe polecat, but also applied to domestic ferret (see below)—Sci. Ed.

^{**}In English, "ferret"-Sci. Ed.

morphology. "M. furo" appeared in southwestern Europe (apparently on the Pyrenean Peninsula) where only M. putorius lives and has lived, and, apparently, from a form which lives (lived?) in extreme northwestern Africa (M. p. furo L., Western Rif; according to Cabrera, 1932; Allen, 1939). This, apparently took place long ago, in a much earlier epoch, when it hardly seemed possible that M. eversmanni could be brought so great a distance to be domesticated. Moreover, there is also no basis to speak of M. furo as an independent species. Some similar features between the skull of M. furo and M. eversmanni are natural, a result of the close relation between M. putorius and M. eversmanni. This may also be the result of some deviations in the skull structure of M. furo as a result of prolonged domestication. Its hybridization with M. eversmanni is the same as the hybridization with M. putorius, but this possibility was extended by domestication (V.H.).

Geographic Distribution

Forest, forest-steppe, and in part steppe zones of the major parts of Europe, and extreme northwestern Africa.

Geographic Range in the Soviet Union

This itself represents the eastern half of the species range.

The western border of the range of the polecat in our country constitutes the state frontier, from the mouth of the Donau [Danube] in the south approximately to 62°40′ N. lat. (northwest of Suoyarva), on the border with Finland in the north.

In Karelia, the northern border extends from this point described above somewhat towards the southeast at first, approximately to the Spassk Bay of Lake Onega, thereby passing around the West Karelian uplands from the south and then, passing around these uplands from the east, it suddenly ascends directly to the north passing in particular, near the western shore of Segozer and reaches Rugozer at 64°10′ N. lat. Thence, the border line turns somewhat northeast and crosses the Lekhta, reaching Kem' on the White Sea (65° N. lat.). This is one of the most northerly points of species' occurrence. The data given apply, on one hand, to the early 1950's, and on the other, concerning the Rugozer-Kem',

to the end of it (Marvin, 1959; Parovshchikov, 1959). Since the polecat is spreading northward, it is possible that its distribution in eastern Karelia after the fifties and the beginning of the sixties has changed and the border extends farther north than is shown.

The White Sea coast constitutes the northern limit of the range throughout its whole extent from the mouth of the Onega to the mouth of the Severnaya Dvina. From Arkhangel'sk, the border goes to the city of Mezen' at the mouth of the Mezen'. In the expanse between Arkhangel'sk and Mezen', the range, apparently, reaches the seacoast and here—almost at the Arctic Circle—attains the other most northerly point inhabited by the species (Mezen', about 65° N. lat.).

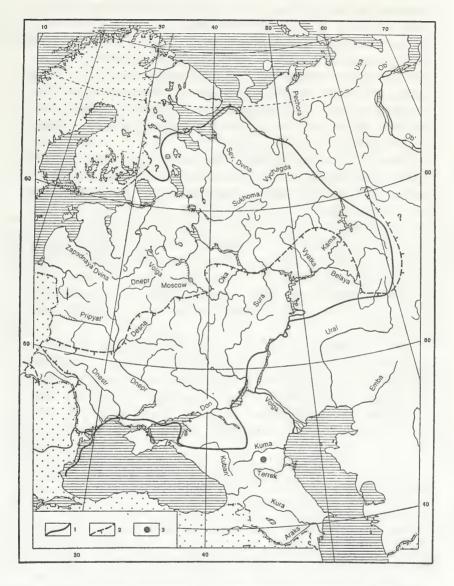
From the mouth of the Mezen', the border suddenly returns to the south and approaches closer to the upper Mezen' in an unclear way (probably along the Mezen') at a place near 64' N. lat. Thence, the northern border of the range goes on, to the upper Vychegda (near 63° N. lat.; V.Ya. Parovshchikov). Farther, the border apparently descends steeply to the south and in the Urals, lies at 58° N. lat. or somewhat more southerly (Shvarts, Pavlinin and Danilov, 1951). However, judging by its distribution on the Vychegda, the border may actually be more northerly.

The eastern border is very poorly known. Apparently, it extends along the Urals, perhaps even to its eastern slopes, embracing Sverdlovsk from the west. Old information on its occurrence in the Irbit region require confirmation.

According to recent data, "forest polecat is absent in Trans-Urals (to the east of Sverdlovsk, V.H.) at the present time" (Stroganov, 1962). Indications concerning former Tyumen, Ishim, Kurgan and Tara regions (Slovtsov, 1892) clearly apply to the steppe polecat, although these are given for "Foetorius foetorius".

The distribution of polecat southward along the Urals is unclear. In the southern Urals (south of the latitude of Magnitogorsk), this species, apparently, does not exist and here only the white polecat is found everywhere (Kirikov, 1952). Information concerning the occurrence of the described species along the eastern slope of the Urals nearly to Orsk (Bobrinskii, 1944) is incorrect.

The southern border of the range begins in the west at the mouth of the Donau [Danube], extends eastward along the Black Sea coast to the mouth of the Dnepr, whence it moves back from the Black Sea coast (to the latitude of Askaniya-Nova) reaching



744 Fig. 265. Borders of the ranges of polecats in the European part of the USSR. V.G. Heptner.

1—range border of forest polecat, Mustela (Putorius) putorius L., 2—western range border of steppe polecat, M. (P.) eversmanni Lesson, outlining the area of sympatry of both species, 3—place of occurrence of forest polecat at Achikulak in the Cis-Caucasus. Question marks in the Trans-Urals,—Irbit, in Kareliya—area of confirmed settlement in 50's and beginning of 60's.

the shore of the Azov Sea, and along it, goes to the mouth of the Don. The black polecat is absent in the Crimea.

In the steppes of the European part of the USSR, the black polecat is rare everywhere, and has a very unique and limited distribution—it is associated only with forest tracts, in part with human settlements and with the edges and valleys of rivers. The farther to the south, the stronger this association. The steppe polecat lives in the open steppe, and in forest very rarely occurs (Askaniya-Nova).

From the mouth and lower Don, the range passes into the steppe of the western and middle Cis-Caucasus. The southern border in this section passes along a line from Stavropol to Krasnodar the western border being formed by the Azov Sea, and the eastern, a slightly curved line directed from Stavropol northwards to Tsimlyansk district on the Don⁴⁸. This latter quite closely coincides with the borders of the Cis-Caucasian steppes.

Details of the border of the range between the Don and Volga are not fully clear. Apparently, it suddenly begins to ascend northward along the Don, and then passes to the Volga somewhat south of Saratov.

In the Saratov steppes of the Trans-Volga, the polecat is absent—it is encountered only in the extreme lower B[olshaya] and M[elenkaya] Irgiz. Farther, the border goes to the north along the Volga. Somewhat south of the Samara bend, it steeply returns to the east and, passing around Obshchii Syrt approximately along 53° N. lat., reaches the Urals at the latitude of Magnitogorsk.⁴⁹

⁴⁸The Cis-Caucasian part of the range is outlined here according to the individual occurrence on the map of Vereshchagin (1956). These points, in turn, were based on data of fur manufacturers. It is not excluded that in some cases, skins were brought from the north. In any event, the black polecat is extremely rare everywhere in the Cis-Caucasus and individuals are met with among masses of steppe polecats. Earlier (Satunin, 1915), its presence in the Caucasus was denied and is sometimes still denied (Kuznetsov, 1952). The possibility is not excluded that this species may penetrate as individual animals somewhat farther to the southeast; for example, it was recorded in Achikulak about 240 km to the east and southeast of Stavropol (V.G. Heptner).

⁴⁹Range after data of Bogdanov, 1871; Slovtsov, 1892; Brauner, 1912, 1914, 1928, 1929; Lobachev, 1930; Ognev, 1931; Isakov, 1939; Bobrinskii, 1944; Vereshchagin, 1947, 1959; Pleskii, 1941; Kuznetsov, 1948; Heptner et al., 1950, 1956; Elpat'evskii, Larina and Golikova, 1950; Marvin, 1951, 1959; Shvarts, Pavlinin and Danilov, 1951; Kirikov, 1952; Korneev, 1952; Sludskii, 1953; Novikov, 1956; I.P. Laptev, 1958; Parovshchikov, 1959; Afanas'ev, 1960; Sokur, 1960; Stroganov, 1962 and others and according to materials of M.Ya. Marvin, V.Ya. Parovshchikov, N.I. Larina, L.G.Turova and V.G. Heptner.

The range of black polecat to the south of the line Zhitomir-Kiev-Orel-Voronezh-Gor'kii-Kirov-Ufa-southern Urals (approximately), *i.e.* in its greatest part, overlaps the range of the steppe polecat. In this region, individual hybrids are encountered (quite rarely), but hybrid populations are not formed anywhere.

The black polecat itself represents a species which is noticeably widening its range towards the north. Its movement is observed in Finland (Kalela, 1952), in Karelia (Isakov, 1939), Arkhangel'sk district and Komi ASSR (Lavrov, 1925, Parovshchikov, 1959), and Kirov district (Lobachev, 1930). There was information that it also colonized eastward—to the Urals and beyond the Urals, but it was decided that this animal passed be-

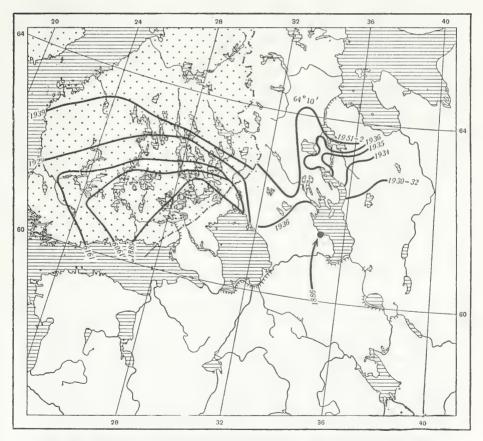


Fig. 266. Colonization of the black polecat to the north in the Karelian ASSR (Isakov, 1929; Marvin, 1959) and in Finland (Kalela, 1952) with additions. V.G. Heptner.

yond the Urals not long ago. However, there are no accurate data concerning its movement in this direction.

The tempo of colonization to the north is quite energetic. Thus, in Karelia, from 1930-1932 to 1956, the polecat colonized towards the northwest about 250 km (from Vodlozer to Rugozer). In Finland, in recent decades the polecat settled nearly all over the southern half of the country (Kalela, 1952). From 1930-1932 to 1956, the polecat settled along the Severnaya Dvina from the latitude of Shenkursk to Arkhangelsk, i.e. for a distance of about 320 km in a straight line (Parovshchikov, 1959). The polecat appeared at Kaisk Pochinki on the Kama at 60° N. lat. at the end of the 20's of this century (Lobachev, 1930) and by 1956, it began to be found, though not often, in the upper Vychegda (Parovshchikov, 1959). Therefore, it moved about 300 km northward or northeastward during a period of approximately 22-25 years. Within 25 years, it moved 300 km along the Onega. Such a tempo of colonization—on average about 10-12 km per year is considered to be very high.

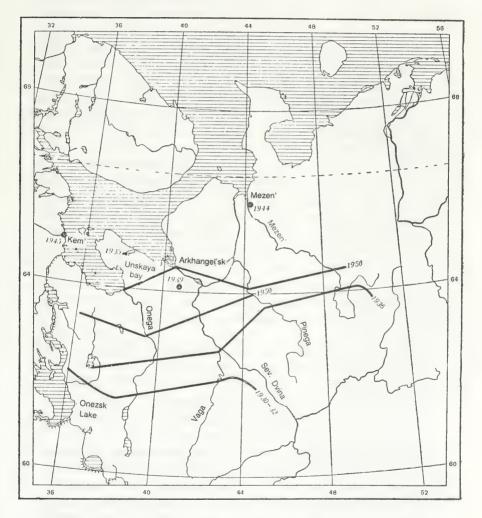
Colonization is mainly stimulated, apparently, by felling of forests and ploughing. However, in some places, it occurs in regions where there are no essential changes taking place in the landscape. Apparently, a certain role is also played by climatic warming which has occurred in northern Europe in places in the last 100 to 150 years. It is considered to be the main cause in Finland. Besides colonization of new places and progressive movement of the border in several segments, a more or less significant "oscillations" of the border occur locally.

Geographic Range outside the Soviet Union

This occupies almost all of Europe. In the north, the border includes Finland south of 66° N. lat.; in the Scandinavian Peninsula, it begins at the Baltic coast at almost 60° N. lat. descends a little westwards including Lake Vattern* from the south, in southeastern Norway, it forms a narrow projection towards the north approximately to 61° N. lat. In the west, the range includes England (absent in Ireland) and in the southwest, it includes the Pyrenean Peninsula and the Rif region in Morocco. The southern border passes along the coast of the Mediterranean Sea (absent on the

^{*}In Russian original, "Venern"-Sci. Ed.

Balearic Islands, Corsica, Sardinia and Sicily). In the Balkans, the range includes the northern part of Yugoslavia; eastward, the border passes along the Donau [Danube], encompassing, however, the Dobruja region (V.H.).



747 Fig. 267. Movement of the northern border of the range of the black polecat in Arkhangel'sk district (Parovshchikov, 1959, with additions). Lines designate the general limits of the range-points—the individual appearance of animals far from the general border. The movement of the border does not fully correspond to that which was established for Karelia. V.G. Heptner.



748 Fig. 268. Species range of the black polecat, Mustela (Putorius) putorius L. V.G. Heptner.

Geographic Variation

Features of the black polecat geographically change negligibly within the borders of our country. It is possible that the black polecats of the steppe zone are somewhat lighter than those of the forest zones (Brauner, 1929). However, these differences apply only to a very small part of the species population in the USSR; they are not yet proved sufficiently and are so insignificant that the southern population does not deserve special designation. If this form is actually distinguished, it is, apparently, identical with the

race rothschildi described from Dobruja (the name orientalis, of Brauner, though earlier was preoccupied, see above in synonymy).

The polecats of the middle and eastern districts of the European part of the country differ somewhat from the western and middle European ones, as well as those occupying the most western parts of the range with us. This, in one form or another was stated much earlier (Satunin, 1895; Brauner, 1929; Ognev, 1931), and in recent times, this was confirmed by some authors, who formally distinguished the East European polecat (Kratochvil, 1952; Polushina, 1955). A series of unclear points were associated with the nomenclature of this form, and thus there was a need for a new name, since the suggested names, including aureus, do not apply to the middle Russian polecats (see note in synonymy of steppe polecat, page 1134 footnote 51 and also Heptner, 1964, 1965).

Within the boundaries of the range of polecats in the European part of the USSR, some geographical localization of the red mutant "P. stantschinskii" is recognized. Individuals of this form are known from Smolensk district (in particular, Roslavl' region), Tambovsk, Moscow district (Klin region), below Ostashkov, Pereslavl'-Zalessk (coll. Z[oological] M[useum of] M[oscow] U[niversity]) and Byelorussia. The name itself, "braginsk polecat, given to this form by fur manufacturers for the city of Bragin (southern Byelorussia), points to a certain geographical restriction.

Within the USSR, two races of the black polecat may be recognized.

1. Middle Russian black polecat, M. (P.). p. mosquensis Heptner, 1965 (syn.—orientalis Brauner, orientalis Poluschina, stantschinskii, ognevi).

Body and skull dimensions relatively small, fur relatively light, slightly fluffy with insignificant luster.

Found in European part of USSR east of line passing approximately through Pskov-Minsk-Zhitomir-Vinnitsa.

Outside the USSR-absent.

Source of above description given of the species is mainly according to material of this form; measurements are of Moscow polecats (see p. 1115).

2. Western black polecat. M. (P.) p. putorius Linnaeus, 1758 (syn.—vulgaris, foetidus).

Body and skull dimensions larger than Middle Russian form, fur darker, lustrous and fluffy.

Found in western part of European territory of USSR to the west from the given line, *i.e.* Pribaltika; Western Byelorussia, western Ukraine.

Outside the USSR, found in central and western Europe.

Differences between the above-mentioned two forms are real, but they are not sharp and are mainly revealed in examination of a series of them. It is entirely probable that characteristics of Middle Russian polecat are associated with its relatively recent colonization of the territory it now occupies (colonization beyond the Ural is, apparently, continuing).

* * *

Outside the USSR, the following forms are usually recognized:

1) M. (P.) p. furo Linnaeus, 1758—extreme northwest of Africa (apparently, does not presently exist in wild state; see above "Systematic position"); 2) M. (P.) p. aureola Barrett-Hamilton, 1904—Spain; 3) M. (P.) p. rothschildi Pocock, 1936—Dobruja, Romania; 4) M. (P.) p. angliae Pocock, 1936—England; 5) M. (P.) p. caledoniae Pocock, 1936—Scotland.

The differences between these forms are, apparently, very slight and require further study. (V.H.).

Biology

Population. Concerning populations of the forest polecat and its distribution within the range, these may be judged by indirect data—the figures of commercial catch. Before the October revolution, about 150 thousand skins of this animal were taken in Russia though locally it was not exploited. In the period up to the Great Patriotic war of 1941–1945, level of the catch increased about 2.5 times on average, and in some places, overexploitation was observed. A rough approximation of the number of polecats in the USSR might be estimated as 200–400 thousand animals.

The distribution of population density within the range may be determined by indices of skin yields in 10 km². Before the revolution, this yield from the entire range was 0.40, and in 1928/29—1.10. The greatest quantity of skins was obtained from Byelorussia. Smolensk, former Valikoluksk, Leningrad, Moscow, and Ivanovsk districts and from the Ukraine. Indices of catch from

these ranged (in 10 km²) from 0.028 in former Severnaya Territory to 4.18 in former Zapadnaya district, 6.28 in B[yelorussian] SSR, and even to 8.70 (region of Verei city, Moscow district). The latter figures already clearly indicate overhunting then. In Germany, these indices fluctuated between 0.43 and 0.77. The forest polecat there was strongly extirpated. Therefore, the greatest density within the boundaries of the USSR is observed in the western part of the range, which is explained by the favorable habitat conditions for this animal there.

Habitat. The forest polecat avoids large, continuous forest massifs. Small forest islands and isolated groves alternating with meadows, cultivated fields and human settlements are more suitable for its life. It is a typical representative of the belt of forest islands and a true "fur-bearing" animal.

Within the boundaries of the taiga forests of the European north, a few polecats are encountered in squatter's settlements, and along the banks of shallow swamps and forest creeks, and they are generally restricted to relatively populated regions. Together with human cultivation and agriculture, it gradually penetrates into the taiga.

In the middle zone, typical habitats of the forest polecat comprise flood lands of small rivers and creeks with their lakes and swamps—the so-called "water" meadows and water-saturated, boggy depressions. Without penetrating deep into the forest, it adheres to openings, borders scrub forest and old clear-cuts, especially those adjacent to worked fields and settlements. Rarely it may be met with in mossy bogs or in deep forests. It settles more often in barns, storehouses, in cattle yards, in cellars of occupied houses, villages and even the outskirts of cities (even cities as large as Moscow).

In the forest-steppe and steppe belts, the forest polecat is restricted to settlements, isolated farms, woody ravines and gorges, and the shrubby floodlands of rivers. Following these latter, it sometimes penetrates deeply into purely steppe regions.

Food. The main food of the forest polecat, everywhere they occur, are mouse-like rodents. Among them, the gray (common) vole [Microtus arvalis] occupies first place (18.5–26.8% occurrence). Red-backed voles [Clethrionomys] are more rarely encountered (4.4–5.5%). In the floodlands of large rivers, the water vole [Arvicola] acquires essential importance (average occurrence about

15%). Of great significance in food of the forest polecat, especially in winter, are amphibians—mainly, grass frog and green toad. These foods have less caloric value, and therefore the polecat never becomes fat from them even when they are plentiful.

Birds occupy third place in food (8–16% occurrence): domestic hens and pigeons, quail, gray partridge, grouse and various small birds. The role of the forest polecat in the destruction of poultry is greatly overestimated. Special investigations showed that in kolkhozes [cooperative farms] and poultry sovkhozes [state farms], losses from it ranges from 0.2 to 2.5% for the adult birds and from 0.5 to 12%, for pullets, most often in the haying period.

Among a number of rare foods of the polecat are the hedgehog, adder [Vipera aspis], grass snake [Tropidonotus natrix] and insects. The significance of individual foods changes depending on fluctuation in abundance of the main food—mouse-like rodents. In case of their insufficiency, the significance of the less valuable food (amphibians) or that of secondary importance, including carrion, increases.

In connection with unevenness in distribution of mouse-like rodents, the composition of food and their ratios are usually different in the separate regions and districts (see Table 68).

In poorly studied summer foods in flooded areas, the water vole predominates (89.1%), further followed by small voles and mice (28.8%), and fish (0.9%) (Grigor'ev and Teplov, 1939).

751 Table 68. Geographic variation in foods of the forest polecat (in percentage of occurrence)

Type of food	Volga-Kama Territory (Grigor'ev and Teplov, 1939)			Middle zone (Lavrov, 1935)
	Summer	Winter		Winter M
	M	lim M		
Mouse-like rodents	28.8	42.0—65.0	25.4	51.2
Water vole	89.1	3.7-32.1	14.7	2.4
Hamsters and ground squirrels		3.3-9.8		_
Insectivores	_	0.8.0	4.1	2.4
Birds		0-12.2	8.0	16.3
Amphibians		0-20.0	12.1	19.5
Fish	0.9	0-16.0	6.9	0.8
Carrion	_	_	wane	9.8
Number of records	114	563	_	123

In the western districts of the U[krainian]SSR (analysis of 111 stomachs and 31 feces), mouse-like rodents predominated in the food of the forest polecat, though the occurrence of all 18 components was not higher than 10% (Polushina, 1958).

	%		%
Hedgehog	1.8	Gray vole	7.6
Shrew	2.6	Domestic rabbit	7.6
Norway rat	6.8	Sparrows	7.6
House mouse	7.7	Song birds	5.0
Harvest mouse	0.9	Bird eggs	3.4
Red-backed vole	3.4	Amphibians	9.3
Mice, Apodemus	6.0	Fish	4.9
Water vole	3.4	Carrion	4.2
Root vole	1.8	Insects	5.0

The forest polecat characteristically makes food stores. The bodies of water where grass frogs overwinter are used as "store-houses" by polecat in the winter time. The polecat continuously visits such places.

Home range. In contrast to the steppe polecat, the forest polecat lead a more settled way of life and has a definite individual home range. However, the dimensions of the range are unknown nor is there data on length of its daily route. Polecats living in villages, among buildings, have a very small home range. In February–March, as a result of food insufficiency, dimensions of the home range noticeably increase. A case is known when the polecat moved about 5 km during a night (Lavrov, 1935).

Burrows and shelters. Forest polecats rarely dig burrows. The permanent burrow dug for them has a simple structure—one short and shallow passage and a small nesting chamber. They sometimes settle in burrows of badger or fox. More often, the polecats use natural hiding places as permanent or temporary shelters—heaps of brushwood, wood-piles, old stumps, haystacks, etc. In villages, the polecat settles under the floor of stables, saunas and other inhabited and uninhabited buildings, and in cellars and storehouses.

Daily activity and behavior. The forest polecat is an animal with a crepuscular and nocturnal rhythm of daily activity. It is very rarely active during daytime, only when motivated by hunger. This is confirmed by laboratory experiments (Kalabukhov, 1943): the

daily rhythm of the forest polecat was shown to be monophasic, with the active period after 20:00 hrs with some reduction at midnight. The indices of the activity of young polecats (2.0–2.5 months) differ greatly: it is equally active throughout the course of 24 hours the day and night, with some increase during daylight hours. The activity of young females during daylight hours is less expressed than in young males.

European polecat is bold and malicious*. It climbs, swims and digs in the earth well, but rarely uses these abilities, being a typical terrestrial carnivore. Its running is less complex and twisting than that of mink and ermine. It is also less quick and evasive than *solongi*, ermine and weasel—man in condition can catch a running polecat. The sense organs are well developed but it cannot distinguish between different colors.

Seasonal migrations and transgressions. Only small seasonal migrations are known but far from all polecats participate. In autumn, many polecats move to villages, attracted by the concentration here of mouse-like rodents after the gathering in of the harvest from the fields. In spring (April), a reverse movement is observed.

Reproduction. As in the steppe polecat, the period of sexual activity extends from the second half of February to the second half of June. Evidently, the rut often extends into April–May (Lavrov, 1935). Duration of pregnancy is 42 days (Moscow Zoo; Manteifel', 1947).

Body length of newborn animals is 7 cm, weight about 7 gm. Number of young in a litter ranges from 2 to 12, most often 4–6 (Lavrov, 1935).

Growth, development and molt. Young polecats are born blind with the ear openings closed by a flap of skin, and covered by sparse, short whitish down. Eyes open on the 34th–36th day; at that time, the wool darkens. Sometimes, the brood does not disperse until spring. Sexual maturity is attained at about one year, but full development and dimensions at two years. Molt in the forest polecat occurs twice annually—in spring and autumn.

Enemies, diseases, parasites, mortality, and competitors. Competitors may be all carnivorous animals and birds feeding on mouse-like rodents: mink, ermine, fox and in recent time, raccoon

^{*}Sic: Russian word is zloba-Sci. Ed.

dog; among birds of prey—the buzzard and owls—and also viper and other [snakes].

In the forest polecat, various infectious and parasitic diseases occur. Bodies of polecats, dying from causes that are usually unclear, are more often found than other carnivores. The forest polecat is susceptible to canine distemper, and it suffers from an unknown infectious intestinal disease accompanied by high mortality. A number of helminths were recorded, including not less than four forms of nematodes parasitizing the frontal sinuses and nasal cavity. In France, distomatosis was revealed in every fourth animal. In some cases, the infection reaches the brain and causes the death of the animal. Usually, many fleas and ixodid mites occur on the forest polecat. In captivity, the forest polecat lives up to 12 years (Manteifel', 1947).

Population dynamics. The forest polecat is characterized by significant fluctuations in numbers. Their cause and character are unstudied. From 1928/29 to 1949/50, i.e. for 22 years, numbers of forest polecat in the southwestern part of Kalinin district increased three times, but to different levels. The increase in the number in 1945/46 was three times smaller than the rise in 1929/30 and six times smaller than the maximum rise of 1938/39.

There is no strict periodicity in the population fluctuations. Apparently, the period is about 7–9 years. Reduction in the population may last from 3 to 5 years, and the growth phase in both mentioned cases equaled 3 years. The sharp and rapid population reduction after 1938/39 occurred at a time of severe summer drought and hard winters of 1939/40 and 1940/41, which caused a sharp and deep depression in the mouse-like rodent population. As a result, the frequency of track occurrences of polecat in the period 1939/40 to 1940/41 fell 9-fold. During 22 years, it fluctuated from 0.03 in 10 km in 1946/41 to 6.03 in 1938/39, *i.e.* by more than 200-fold. In the post-war years, the polecat population (as well as of ermine) was low everywhere, but the cause of this was unclear.

Field characteristics. Tracks of the forest polecat are 1/3 smaller than marten, its jump is equal to 40–65 cm and prints of claws and callosities of the feet are very distinct (Formozov, 1952). For differences from tracks of mink, see page 1106. Triple prints of the feet are as typical for the forest polecat as pairs. When walking, it frequently changes feet, and often one pace for another. The general character of the track or trail is distinguished by an absence

753



753 Fig. 269. Tracks of the hind and fore feet of black polecat on silt. Shore of Moscow river, Zvenigorod. 22 June 1939. Sketch by A.N. Formozov, about 2/3 natural size.

of elaboration typical of the mink. It moves in energetic leaps, digs in places inhabited by mouse-like rodents, and prefers to catch animals moving on the surface, so rarely digs in the snow. Its track is not so tangled as weasel and ermine (Formozov, 1952) (P.Yu.).

Practical Significance

The forest polecat is a valuable fur-bearing animal. The price of its skins is higher than that of steppe polecat. The fur enjoys a good demand on the world fur market on which, before the 1914–1918 war, Russia offered more than 50% of all skins. After the October revolution, the take of this species in the whole USSR increased noticeably as reckoned by growth of the catch, and also as calculated by a decrease in its number in western European countries. In the years after the Second World War, our population of this species decreased somewhat. This was reflected in the volume of catch of the forest polecat. In 1956–1969, as compared to 1926–1929, its take decreased on average in the European part of the USSR from 30% to 7.2% *i.e.* by about four times (Danilov, 1963).

Considering this, and the utility of the polecat in destroying harmful rodents in fields and settlements, attention must be paid to husbandry of the stock of this carnivore. Damage caused by it to poultry is overestimated and can be easily brought to a minimum with proper construction of poultry yards.

The forest polecat is hunted chiefly in late autumn and in the beginning of winter by guns and dog, as well as with jaw traps and various wooden snares or traps (*cherkan*, *plashki* and others). Hunting with dogs is the most efficient. In a season, the hunter rarely catch more than 10–15 polecats. The animal does not serve as an essential element in commercial hunting, and for the most part incidentally captured.

It is necessary to restrict the hunting of the forest polecat to the period of complete "primeness" of its skin, and not to allow its extirpation in the hunting season (P.Yu.).

STEPPE, OR WHITE, POLECAT

Mustela (Putorius) eversmanni Lesson, 1827

- 1827. *Mustela eversmanni* Lesson. Man. de mammal., p. 144. Region of Khobda river depression in Ilek, south of Orenburg (Stroganov, 1962).
- 1849. Putorius larvatus Hodgson. Journ. As. Soc. Bengal, 18, p. 447. Utsang in southern Tibet, north of Sikkim.
- 1910. Putorius eversmanni Lesson var. michnoi. Kastschenko. Kashchenko. Ezhegodn. Zool. muzeya Ak. Nauk, 15, p. 271. Kiran river 20 km from Troitskosavsk (Kyakhta), Trans-Baikaliya.
- 754 1912. Putorius eversmanni sibiricus Kastschenko. Kashchenko. Ezhegodn. Zoolog. muzeya Ak. Nauk, 17, p. 395. Aginsk steppe, Trans-Baikaliya. Nomen nudum. Nec Mustela putorius sibiricus Radde (= Mustela sibirica Pallas). Name given with authorship of Radde (1862)⁵⁰.

So Kashchenko's uses of the cited name is evidently a misunderstanding. Radde (1862, p. 42), while describing the Transbaikal polecat which he called Mustela putorius and referring to its characteristics, emphasizes that its guard hairs are not black but as reddish as those of "Mustela putr. sibirica" as Radde writes. It is quite clear that Radde had in mind the kolonok, Mustela sibirica, but the addition of the incomplete word "putr." is a simple slip of the pen, a strange form appearing in this context. Therefore, to consider that Radde described a special form of polecat as is accepted by Kashchenko, has no foundation at all. Moreover, in the same text of Radde, there is nothing all that can be interpreted as a description of a new form. It is very strange that Kashchenko, after describing one form of polecat (michnoi) from Troitskosavsk (Kyakhta), noted another for the Aginsk steppe, i.e. from the nearest neighborhood. In the work of Kashchenko, there is nothing resembling a diagnosis. Apparently, he had a winter individual in one case, and in the other—a summer, or an unmolted one.

- 1913. Mustela lineiventer. Hollister. Proc. Biol. Soc. Washington, 26, p. 2. Chagan-Burgazy, Chuisk steppe, southern Altai.
- 1928. Putorius eversmanni satunini. Migulin. Zh. "Ukrainsk. mislivets ta ribalka", No. 9, p. 30. Nogaisk steppe, northeastern Cis-Caucasus.
- 1927*. Mustela eversmanni robusta Ehik. "Nimrod", 10. Hungary.
- 1928. Putorius eversmanni talassicus. Ognev. Memuary Zool. otd. Obshch. lyubit. estestv., antropologii i etnogr., 2, p. 26. Talassk Alatau.
- 1928. Mustela eversmanni hungarica Ehik. Ann. Mus. Hist. Nat. Hung., 25, p. 37. Mad'yarovar, Hungary.
- 1929. Putorius eversmanni occidentalis. Brauner. Zh. "Ukrainsk. mislivets ta ribalka", No. 2-3, p. 9. Khersonsk gov.
- 1930. Putorius eversmanni amurensis. Ognev. Zh. "Okhotnik", No. 11, p. 25. Blagoveshchensk on Amur region.
- 1936. Putorius putorius aureus. Pocock. Proc. Zool. Soc. London, p. 703, Kazan.⁵¹
- 1958. Putorius eversmanni nobilis. Stroganov. Izv. Sibirsk. otd. AN SSSR, 11, p. 150. Vic. of Kokchetav, Kazakhstan.
- 1958. Putorius eversmanni pallidus. Stroganov. Ibidem, p. 150. Kargat, between Novosibirsk and Lake Chana.
- 1958. Putorius eversmanni tuvinicus Stroganov. Ibidem, p. 152. Chaa-Khol' village, Tuvinsk depression.
- 1958. Putorius eversmanni dauricus. Stroganov. Ibidem, p. 154. Smolenskoe village, near Chita, Trans-Baikaliya.
- 1960. Putorius eversmanni heptapotamicus. Stroganov. Tr. Biolog. inst. Sibirsk. otd. AN SSSR, 6.** Ili river, southern Pribalkhash'e (V.H.).

Diagnosis

General color light, whitish-yellow, only weakly overlaid with blackish-brown (dark guard hairs). Middle of belly light, some-

^{*}Out of chronological order in Russian original—Sci. Ed.

⁵¹Belongs to the steppe polecat group. The place where the type was captured is, apparently, not accurately reported, or is incorrect—the individual was received by the British Museum from Latast, *i.e.* captured in those years when the steppe polecat was absent near Kazan. As can be determined by the description and drawing, it is possible that the type (the only specimen) is itself a hybrid of the black and steppe polecats (V.H.).

^{**}Page number not given in Russian original-Sci. Ed.

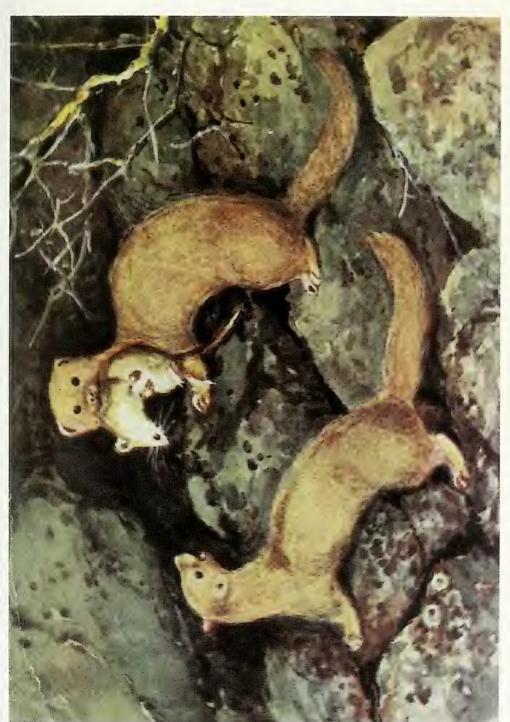


Plate 8. Transbaikal solongoi, Mustela (Mustela) altaica raddei Ogn. Painting by A.N. Komarov.



times with narrow, dark, longitudinal medial band, lower surface of neck, chest, posterior part of abdomen and inguinal region brown in color. Base of tail light, only terminal part dark-brown. Postorbital constriction of skull well marked—narrower than interorbital (V.H.).

Description

The white polecat is entirely similar to the black in general appearance, proportions and habits, but its body appears somewhat more elongated. Possibly, this is due to guard hairs, especially those on the posterior part of the body, being not so long and luxuriant. The tail is quite short and constitutes about one-third of body length, covered by short close-lying hairs, and on the whole, is not very fluffy and appears quite thin.



Fig. 270. White, or steppe, polecat, Mustela (Putorius) eversmanni Less. Sketch by A.N. Komarov.

755

Winter fur tall and soft, as a rule, with dense short underfur characteristic of polecats and sparse long guard hairs. Length in both one and the other, however, is usually less in steppe polecat than forest polecat. Also less is general thickness of pelage layer. On the whole, fur of steppe polecat is somewhat coarser than forest polecat. Guard hairs more strongly developed and denser in posterior portion of dorsal region. At the same time, they are sparser than in forest polecat and contrary to the case found in that species, guard hairs never completely cover the underfur, whose color determines the animal's color on the entire body.

Anal glands well developed, their secretion has same sharp smell as in black polecat and, apparently, also can be sprayed (no direct information on this).

Teats, 3-5, usually 4 pairs.

General basic color tone of winter fur very light, yellowish or whitish-yellowish, determined by underfur color. Over this background, is a more or less significant dark frosting formed by blackish-brown or brown ends of guard hairs (their bases are light). This frosting is stronger in middle and especially posterior parts of the back, where guard hairs are denser and longer, having a longer dark part, and it is more intensively colored. In anterior part of back, in the region of shoulder blade and along upper neck, this frosting, forming a sort of "two-layered" fur color, is weaker and may be almost undeveloped or even absent. Guard hairs here are extremely short. On the sides of the body dark frosting is also considerably more weakly developed than dorsally.

Head piebald in color—chin, lips and cheeks white; eye region, expanse between them and dorsal side of nose covered by brownish field (mask). Posterior to mask, crossing head from cheek to cheek runs a white band; in front of each ear, a small dark area of the same color of the mask is usually located. Occiput, region between ears and dark part of head usually has color of upper neck, on the whole forming dark area on head demarcating posteriorly the white transverse band. Ears completely white, throat yellowish-whitish or almost white. Character of head pattern very variable both in color and in area of different color field. Mask often narrow and pale, dark region is light and whole head light. Sometimes, head is entirely white or almost white (slightly ocherous) and head pattern is absent.

Lateral parts of neck of same color as anterior part of sides or lighter; its lower surface, posterior to throat dark, blackish-brown or brown. Chest and forelegs black or blackish-brown; Venter light, yellowish-straw; its posteriormost part, inguinal area and posterior extremities dark, black-brown—as in fore limbs. Basal part of its tail (half or two-thirds) has light color tone like that of sides; distal part brown or black-brown, almost black.

Vibrissae black and white; hairs covering soles of feet close-fitting and elastic, black-brown and hiding digital callosities and foot pads. Claws light-horn [in color].

Fur color is subject to very great variation, first of all being individual. Its general tone may be either lighter or less light, sometimes almost white, or with greater or lesser ocherous tinge. Differences in density and intensity of guard hair color exist, as do, consequently, intensiveness of dark frosting on basal light "deep layer" of color. Degree of development of guard hairs and darkening in the anterior part of body, it is generally said, are weak, sometimes disappear, and then, not only head but also the neck and even anterior part of trunk are white or almost white. Intensity of dark fields on ventral body and, to a lesser extent, on tip of tail, is subjected to significant individual variability. Often, there is a median line on the venter, a narrow dark stripe extending between dark areas on chest and groin.

Summer coat shorter and coarser than winter, and is not as dense and close-fitting. Ocherous or reddish tone strongly developed. On head, especially around eyes, brown tone more strongly developed. On the whole, head darker than in winter; contrast between dark and white sections sharper and it appears more piebald. As in winter fur, color contrast on head is sharper in younger animals. In other respects, summer color corresponds to winter.

Sexual differences in color are absent.

Newborn polecats are naked, but in first days of life they begin to acquire, as in black polecat, a pelage of short white hairs. At approximately 10 days of age, limbs, forehead and back begin to darken, and then facial mask becomes distinguishable and the animal gradually receives a coat similar to adults, but duller, and formed by "underfur-like" hairs. Its full development of head pattern, *i.e.*, dark mask, light (white) cheeks, white band behind mask and dark crown and forehead, is attained only in first winter pelage.

In steppe polecat, the process of pattern development begins earlier and proceeds more quickly than in the forest polecat, and it is already fully developed in the subadult individuals (Kratochvil, 1962). In polecats of intermediate age, mask and entire head pattern are well-manifested—they are relatively clearly outlined and densely colored. With age, the whole head lightens, parietal and occipital parts disappear or become paler, their area decreases and the mask tone lightens. In the very old polecats, head is perhaps entirely white, or even silver in tone, and traces of mask are unnoticeable or hardly developed. As noted, anterior part of trunk and neck strongly lighten. With age, general tone of underfur lightens, which may lead to almost white [pelage] with light straw-colored frosting.

"Exotypic" variations which are so sharp in black polecat are not noted in the steppe, or they are rare. In particular mutations like the "braginsk" polecat have not been described.

Geographic variation in color, in contrast to that observed in black polecat, is better manifested, and reveals itself in degree of intensity of general tone of underfur (it may be almost white) and guard hairs, degree of development of ocherous and reddish tones, density of dark ventral color, head and neck color, development of facial pattern, length of black tip of tail, etc. Therefore, well-known parallelisms of not only individual and age variation, but also geographic variation is manifested. Density and length (quality) of fur also changes geographically.

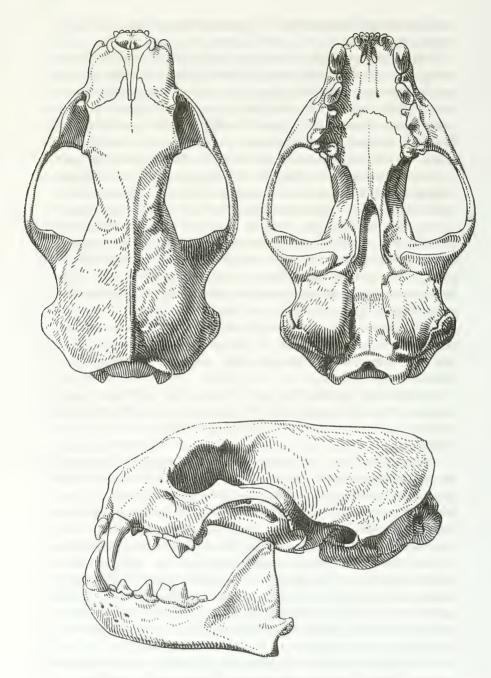
Skull coarse and heavy—heavier and more massive than in forest polecat. It is relatively wide, with wider braincase and more widely separated zygomatic arches, and on the whole appears shorter and wider than black polecat, especially in braincase region. Mastoid width usually considerably greater than half condylobasal length of skull. Protuberances, crests, etc. of skull more strongly and sharply developed than in forest polecat, especially occipital crest, and also sagittal. Also well developed is its anterior branch, extending to supraorbital processes, which, as in the mastoids sharply expressed. Zygomatic arches strong and particularly widely separated in posterior portion. Zygomatic width in adult and old individuals usually exceeds mastoid width. Interorbital area forms clear convexity on line of upper skull profile, from which profile line of facial portion quite abruptly descends downwards. On the whole,

skull somewhat flattened, but in posterior region less so than in black polecat.

Facial part of skull is not large, but is relatively larger and stronger than that in black polecat. Interzygomatic part of cranium very narrow and extended. Lateral outlines of its postorbital part not parallel, but form two lines which meet at an angle in a sharp constriction (interception; "waist") and behind it, again diverge. Width of this part in its narrowest place is less than interorbital width—in old individuals considerably less. Most constricted part in postorbital area, with closed jaws, usually lies in front of line uniting apices of coronary processes (see the note on page 1113). External nares not compressed laterally; their width usually equal to their height. Auditory bullae in posterior half not swollen or swollen to lesser degree than in forest polecat; carotid foramen lies in middle of longitudinal inner border of auditory bulla. Ends of pterygoidal processes do not form strongly recurved external hook. Nasal bones wide anteriorly, posteriorly narrowing to a quite pointed wedge extending between anterior portions of frontals, and, in general, similar to black polecat. Dentition similar to black polecat but stronger and teeth, most of all canine and carnassial teeth, generally more massive. In connection with this, lower jaw also somewhat more massive.

Female skull differs from skull of male (not to mention measurements) by less sharply defined protuberances, crests, etc., and in having somewhat smoother outlines. It is lighter, with somewhat weaker teeth.

In young polecats, postorbital constriction not sharply defined; the younger the animal, the weaker. Moreover, it lies more anterior, closer to supraorbital processes. Braincase more swollen and narrower posteriorly, without crests or only just noticeable. In connection with relatively wide interzygomatic area, whole braincase appears elongated and swollen. Skull of young steppe polecat very similar to skull of black polecat of same age. Some features of this similarity are retained in older animals but there is another age correlation—the skull of the subadult steppe polecat is similar to that of a more mature black polecat in some respects (chiefly, structure of interzygomatic area). Further, in connection with constriction of postorbital area and development in it of an "interception" species differences are projected all the more sharply. The course of age variation in the skull of steppe polecat,



758 Fig. 271. Skull of steppe, or white, polecat, Mustela (Putorius) eversmanni Less.

759 therefore, in a purely morphological sense, is considerably greater than in the forest polecat. With time, apparently, such an essential difference is absent, or is not proportional to the degree of morphological differences. Apparently, the tempo of age changes in the steppe polecat is more rapid. In one way or another, the contrast in skull structure of young and extremely old steppe polecats (with almost obliterated teeth) is much greater than that in black polecats of their respective ages.

As a very rare individual structural deviation, there is in the skull sometimes a bony connection between the end of the pterygoidal process and the bony auditory bulla.

The os penis shows the same characteristics as in the black polecat, but differs somewhat in measurements (see below).

The amplitude of variation of measurements of the steppe polecat is very great and is, in general, greater than in the black polecat. This is, apparently, associated not only with the longer growth period in the steppe polecat, but also with some geographic variation in this character, which does not occur, or is less marked in, the black polecat. Moreover, the range of the white polecat within the boundaries of our country include regions where exploitation is practically undeveloped, and the animals live to the end of life, or in all events, grow to their maximum limit. The black polecat is hunted quite intensively everywhere.

As in black polecats, giant individuals are encountered among white polecats, the measurements of which extend beyond the limits of "normal" fluctuating variation in the species. They are met with significantly more often, at least in some places, than the black polecat. They are most of all found in western Siberia⁵². No literature exists with information about giant polecats in other parts of the range. Since unusually large kolonok (see page 1057) sometimes bear polecat features (dark-brown tail end and brown feet; I.M. Zalesskii, 1930), it is not excluded that the giant polecats (as well as kolonok) are intraspecific crosses (in western Siberia, both species live together and often in one biotope) and their size is an expression of the phenomenon of heterosis. Giant polecats (as also kolonok) are known almost only from their hides, and are nearly unstudied.

⁵²In the steppes along the upper Irtysh, they are even known to the local inhabitants who call the abnormally large polecats "mogil'shchik" (=grave digger) because of the belief that they live in graveyards and feed on the dead (Zverev, 1931).

Sexual dimorphism in dimensions is quite sharp—female body length consitutes about 85-90% of male, and weight averages about 45-50% of male weight.

Body length of males is 320-562 mm, of females, 290-520 mm; tail length of males is 80-183 mm, of females, 70-180 mm, length of hind foot of males is 40-80 mm, of females, 35-72 mm (from 1611 specimens: 1,237 specimens—671 males and 566 females from Zverev, 1931; 374 specimens from Stroganov, 1962); length of ear of males is 23-26 mm, of females, 20-23 mm (Stroganov, 1962).

Condylobasal length of male skull is 61.7-82.2 mm, of females, 52.4-76.7 mm; zygomatic width of males is 30.0-58.9 mm, of females, 30.0-48.7 mm; mastoid width of males is 35.7-47.9 mm, of females, 35.3-43.2 mm; interorbital width of males is 15.9-24.2 mm, of females, 14.0-19.5 mm., postorbital width of males is 12.0-17.2 mm, of females, 11.3-15.3 mm (Stroganov, 1962; values given by Ognev, 1931 and Novikov, 1956, do not cover the full amplitude of variation of body and skull dimensions).

Os penis length of adult males (7) is 36.7-M39.1-42.5 mm, of young (30), 33.9-M36.6-40.6 mm; weight of bone in adults is 0.370-M0.436-0.530 gm, of young, 0.130-M0.200-0.280 mm (V. Popov, 1943; material from Povol'zhe). Even with some transgression in length, no transgression in weight of both age groups is observed).

Weight of Siberian males up to 2,050 gm, of females, 1,350 gm (Stroganov, 1962).

One giant polecat had a body length without tail of about 760 75-80 cm, although normal dimensions of animals from this region (in particular Semipalatinsk) is about 40 cm, and in rare cases 42-45 cm. It was taken in Semirech'e. Its color was completely typical for southern Siberian steppe polecats, but its fur was coarser and its skin "extraordinarily thick" (Zverev, 1931) (V.H.).

Systematic Position

The steppe polecat is undoubtedly very close to the forest polecat. The proposal to unite them into one species (Pocock, 1936) was supported by many, although not all, West European zoologists having at their disposal, genally speaking, only insignificant material of the white polecat. The idea was not met sympathetically by us. Actually, if all features and properties of both polecats are

evaluated, and the question is approached not only from a purely morphological point of view, it is evidently correct to consider them different species. Even if we consider that the correlation of these two forms (a group of forms) itself represents a "borderline case" between species and subspecies in which either view might seem right, nevertheless in final consideration, the large argument favor the treatment employed here—M. (P.) putorius and M. (P.) eversmanni⁵³.

Concerning skull structure, the white polecat itself represents a farther step of specialization in the direction of carnivory as compared to the black. The white polecat has stronger dentition, protuberances, crests, etc. are better developed and the masticatory ("predatory") musculature is much more powerful. Concerning this, one can judge from the whole structure of the sharply compressed postorbital region indicating the degree of development of the corresponding muscles. Possessing no essential differences in body structure, the white polecat as a whole, and in several of its individual races, is larger than the black polecat. It is naturally assumed that all of this is related to larger prey. The close connection of this polecat with ground squirrels and apparently even marmots in some places is better recognized and understood. It is associated with murid rodents to a lesser extent than the black polecat and, apparently, is completely independent of amphibians.

The course of age changes in both species shows that their skulls are very similar in early age—no essential differences exist between them in the interzygomatic region. Later, in the black polecat, the above-described structure of the interzygomatic region is formed, and at this age changes in this region terminate. As mentioned, these changes go farther in the steppe polecat, with significant changes appearing, all strengthening with age, and leading to sharp differentiation from the structure characterizing the black polecat. In very old individuals, the general appearance of the skull has little in common with the skull of the black polecat—less than with the skull of mink. Therefore, the chain of age changes in the white polecat is longer and leads to much greater differences between the skulls of old and young than in the black. Somewhat schematically speaking, the skull of the adult black polecat corresponds with the subadult white polecat, and bears recogniz-

⁵³For details of the whole question both morphological and geographical sides, see Heptner (1964).

able infantile features. This relates even to old males, not to mention females and males of younger ages at the same chronological stage as white polecats. The correlation is approximately as in European and American mink, but the differences in morphology of the final stages are greater.

Geographic features of both species obviously give evidence for their treatment as independent species. However, if the entire range of both species is taken into account, a definite geographical 761 vicariance is delineated, although the region of sympatry of the two species is great. Together with this, the boundary "transitional" belt is not narrow, but a significant part—about one-third if not more of the range of the black polecat—is covered by the range of the white (the reverse correlation is different). Both species exist in this region of mixing, in a known degree of independence, inasmuch as there is the general possibility for mammal species with this type of ecological isolation. The steppe polecat confines itself to open expanses, and the forest—closed biotopes or human settlements. In the southern European part of the USSR, the black polecat penetrates into the steppe zone chiefly along the valleys of rivers, and in the steppes, with ground squirrels, the white polecat lives. Thus, along the Dnestr [river], in its lower course, the black polecat lives in the valley, and nearby in the steppes, the white polecat (Brauner, 1929); in the Carpathians, in the mountains—the black, and to the south in the Carpathian plain—the white (Konyukhovich, 1953), etc. Both species exist together in Czechoslovakia and Austria, but in different biotopes (the white—in steppetype biotopes with ground squirrels) (Bauer, 1960; Kratochvil, 1962). They also colonized the Russian plain in the east and north (see later); the white polecat, as said, freely penetrated into the region inhabited by the black. Therefore, there has been unlimited contact between both species in the region of their sympatry of inhabitation nonetheless. This is not contradictory in that in floodland biotopes in some regions (Tatariya), their sympatry has been recorded repeatedly (V.A. Popov).

With all of this, black and white polecats give natural hybrids. This is entirely natural if we take into consideration the possibility of hybrids of white polecat with kolonok and hybrids of the black polecat with mink—forms the species independence relative to the polecat is undoubted. However, crosses of both polecats are of far lesser magnitude than one might expect from their sympatry and

systematic proximity, and generally speaking, are quite rare. They have been noted in a series of places—in the southern Ukraine, in Kursk and Voronezh districts, Trans-Carpathians and several other places. They are known not only to furriers, but also zoologists⁵⁴.

At the same time, in their entire territory within the limits of the USSR (apparently, and outside the USSR) black and white polecats are encountered together, and nowhere do they produce hybrid populations, and a zone of transgression between the two species is absent. Only rare individual interspecific hybrids occur. For Czechoslovakia and Austria they are not even recorded (Bauer, 1960; Kratochvil, 1962). In recent times, some western authors, on the basis of their own observations in Central Europe, and considering the views of our taxonomists, recognize two species of polecats (Bauer, 1960; Kratochvil, 1962)⁵⁵.

The North American ferret* $(M.\ (P.)\ nigripes\ Audub.$ et Bachon.) is close to the steppe polecat of the Old World. Their skulls are similar not only in main features, but also in all fundamental details (Pocock, 1936) including general dimensions and dimensions of the separate parts. The only difference lies in the color—the ventral side (except legs) in $M.\ (P.)\ nigripes$ is light. However, in several individuals a weak darkening is observed in the chest region, lower part of neck and inguinal region. It is entirely likely, that if the whole range of variation of all races of steppe polecats of Eurasia were evaluated, $M.\ (P.)\ nigripes\ must$ be considered as only a subspecies of $M.\ (P.)\ eversmanni$. If we were to unite $M.\ (P.)\ putorius\ and\ M.\ (P.)\ eversmanni\ in one species, then to give species independence to <math>M.\ (P.)\ nigripes\ in$ no way permissible (V.H.).

Geographic Distribution

Found in Central and in part in Middle Asia, Kazakhstan, southern Siberia; southern and in part middle parts of eastern Europe and Central Europe.

⁵⁴It is possible that one such hybrid, as far as can be judged by the description and drawing of the skull, was used in the description of the form *Putorius putorius aureus* from Kazan and was used as a reason to unite the species *putorius* and *eversmanni* in one species (Pocock, 1936).

⁵⁵For the systematic interrelationships of polecats and related species of Eurasia, see also the corresponding sections on black polecat, mink and kolonok.

762

^{*} The common name in English is black-footed ferret-Sci. Ed.

Geographic Range in the Soviet Union.

Range is great and constitutes a considerable part of the range of the species, namely its western and northern parts.

The most westernly place of occurrence of the white polecat in the USSR lies in the Trans-Carpathian district, where it was recorded in the Uzhgorod and Mukachev regions (Kratochvil, 1962; Konyukhovich, 1953). Apparently, it occupies the entire Trans-Carpathian plain, but is absent in the mountains. This area of occupation of the white polecat is isolated from the remaining range of the species within the boundaries of our country and is connected with its central European part lying in Czechoslovakia, Austria and Hungary. [This section] constitutes its northern edge, bordered on the north by the Carpathian [mountains]. Its union with the remaining range is made through Romania and the region of the lower course of the Dnestr (see later).

To the north of the Carpathians, the northern limit of the range of the steppe polecat begins in the Ravy-Russkaya region at the Polish border north and northeast of L'vov (Tatarinov, 1956). Thence, it passes south around Lutsk and Rovno, going on to Zhitomir and farther to Kiev (Sharleman', 1915) extending, evidently, somewhat to the north of it, and reaches Nezhin (Ognev, 1931; Sokur, 1960) or, more probably, to Chernigov. It is not excluded that in the expanse west of the Dnepr, the white polecat is locally distributed in areas lying to the north, although positive data on this are absent, and in Byelorussia, this species is not encountered (Serzhanin, 1961). Its spread to the north, going on in the more easterly parts of the range has not been noticed here, or is less intensive.

Farther to the east, in the expanse between the Dnepr and the Ural mountains, the species being described had already spread northwards quite long ago (see later), and especially intensively, apparently, in the last decade. Therefore, information on the northern limit of its range here is not always fully defined.

At the beginning of the 60's, it was accepted that from Chernigov the borderline steeply ascends to the northeast, directing itself towards Bryansk and even somewhat northwest of it—to Zhukovka (Yurgenson, 1932). Thence, the border of the range

extends almost directly eastward—to Telech'e* to the north of Orel (F.F. Rudnev) or even to Kaluga and from there to Tula, Ryazan' and Gork'ii (Kuznetsov, 1952); *i.e.*, approximately along the Oka [river]. According older data, the occurrence of the steppe polecat was recorded south of the line leading eastward from Orel, at Chaplygin (Ranenburg), northwest of Tambov, at Morshansk north of Tambov (Vyazhlinskii, 1928) and at Kuznetsk (Ognev, 1931)⁵⁶.

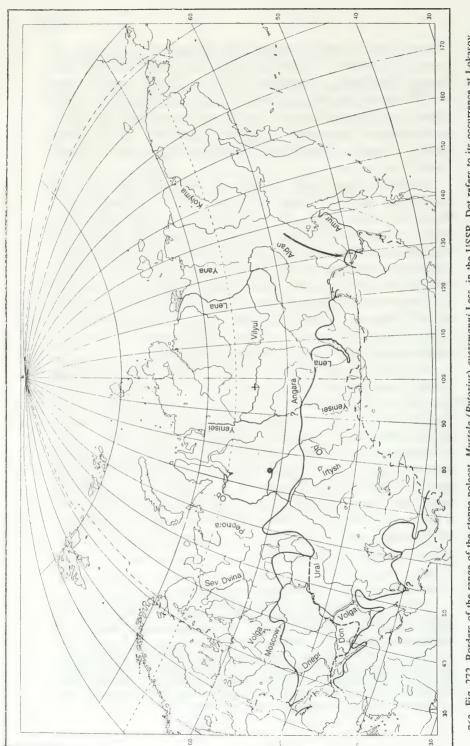
Between Ryazan' and Gork'ii, the borderline takes a great bend to the north into Vladimir district. Here, in the beginning of the 60's, in this region, the white polecat was met with everywhere, even the most northern regions of the district and was not recorded only in the very northwestern bordering Moscow, Yaroslav and Ivanov districts—in Aleksandrov—and in one of the southwestern [regions]—Kurlovsk (in Vladimirsk Meshcher to the west of Shatura and northeast of Spas-Klepikov; according to the data of N.D. Sysoev). According to these data, the occurrence of the white polecat in Moscow district is probable, especially since it is not exclusively a rarity in Vladimirsk (see later).

It is possible that the light [white] polecat penetrated into the southern parts of Gork'ii [in] Zavolzh'e and exists in this district not only south of the Volga. In any event it was recorded not only for Chuvash, but also in the eastern part of Mari ASSR (Yurgenson, 1932). Therefore, reaching the Volga somewhere above the mouth of Kama, the borderline directed itself quite steeply to the northeast, covering not only the entire Tatarsk Republic, but also the southern part of Kirov district. In an unclear way it is directed closer to Omutninsk (58°40′ N. lat. and a little east of 52° E. long.; Popov and Lukin, 1949). This is the northernmost point inhabited by the species in the European part of the country.

^{*}In Russian original, misspelled "Telyache"-Sci. Ed.

⁵⁶Due to technical reason, the maps published by Heptner et al. (1950, 1956) contained an error—it contained no data on the occurrence of the white polecat in Moscow district and is absent in Smolensk. In agreement with the new data, the border in the east extends in a different way.

In some maps of the range in the European part of the USSR published before the present time, their transgressions were very great (Bobrinskii, 1944; S. Naumov and Lavrov, 1948). This concerns also some other parts of the range, especially Priural'e, Priamur'e and Middle Asia, through which the data of the maps (Bobrinskii, 1944) in particular do not correspond with the actual situation.



763 Fig. 272. Borders of the range of the steppe polecat, Mustela (Putorius) eversmanni Less. in the USSR. Dot refers to its occurrence at Lokasov on the Ob'; cross refers to erroneous indication at mouth of the Viv'; arrow directs attention to the part of the range on the left bank of Amur. The dotted line refers to the southern border of the region where Siberian and European polecats occur in sympatry. V.G. Heptner.

To the east of the European part of the USSR—in Priural'e and in the Urals, the border of the range is very poorly clarified. From Omutninsk, it apparently is directed towards the Urals (the white polecat does not reach the northeastern parts of Perm district; Kuklin, 1951) and along its western foothills, and encompassing Tatarsk Republic from the east, which the white polecat entirely occupies (Popov and Lukin, 1949), steeply descends to the south. Southward, the border apparently extends approximately along the Ufa and Belaya [rivers]. At the latitude of Magnitogorsk, or slightly northward (53° 30′–54° 00′), the border turns sharply to the east and crosses the Urals. The assumption that the northern border of the range passes through the Urals below 58° N. lat. (Yurgenson, 1932), i.e. that the steppe polecat lives all over the middle and southern Urals, is apparently wrong.

In the Trans-Urals and western Siberia, the border at first passes northwards along the eastern slopes of the Urals through Miass (west of Chelyabinsk) to Sverdlovsk and, going farther to the north, reaches approximately 60° N. lat. in the upper Sos'va (Kuklin, 1938; Shvarts, Pavlinin and Danilov, 1951; Laptev, 1958; the northernmost point inhabited in Asia). Along the Sos'va, the border goes to the southeast and reaches the middle and lower courses of the Tavda, and turning towards the northeast, it passes farther to Tobol'sk or to a point a little north of it. But, its occurrence so far to the north in Trans-Urals sometimes gives rise to doubts (Stroganov, 1962), and it has been assumed that the border of the range from Sverdlovsk goes to Irbit and thence even to Tobol'sk. In any event, in Trans-Urals the polecat does not reach Ivdel' (60° 40′ N. lat.).

From Tobol'sk, the border line, generally following the Irtysh, or going a little to its north, directs itself east approximately to the mouth of the Shish river and there it turns to the sources of Vasyugan (I. Laptev, 1958), including, in this way, the entire basin of the Tara (Yakushevich and Blagoveshchenskii, 1952). From the source of Vasyugan, it again extends to the east or, somewhat deviating to the north, and reaches the Ob' (the polecat is absent to the north of the Vasyugan basin) somewhere between the places where Vasyugan and Ket' flow into it (I. Laptev, 1958). Farther, the border goes on to the Chichka-Yul river and crosses the upper Ket' and Kem' (V.N. Nageev) to reach the Yenisei between Krasnoyarsk and the mouth of the Angara, perhaps at Eniseisk (Kuznetsov, 1952).

Individual animals sometimes, apparently, go beyond the described border, but long transgressions are very rarely seen. Thus, the polecat was recorded at Narym (Ognev, 1931) and in 1947, one polecat was taken on the Ob' at Lokosov (Lokusov), somewhat above Surgut (I. Lapteev, 1958). If this is not a collected skin [from elsewhere], then it most probably is a traverse along the Ob'valley.⁵⁷

To the east, in the Yenisei basin (Irkutsk district), the northern border of the range of the steppe polecat advances across the Shitka region to Biryus (a little north of 56° N. lat.) and Bratsk on the Angara, and rising slightly to the northeast reaches Ust'-Kut on the source of the Lena. Thence, it somehow descends to [Lake] Baikal without passing around it from the north. For the Yenisei basin, there is evidence of the capture of a polecat at the confluence of the Viv' river with the Nizhni [Lower] Tungusk (at 64°; Yakovlev, 1930; Ognev, 1931); this is a poorly understood mistake—the range undoubtedly does not extend so far.

To the east of Baikal, the range on the north includes the region of the left tributaries of the Vitim, the Amalat, Tsipa and Tsipikan rivers, and reaches the upper Angara (Bauntovsk and Severo Baikalsk regions of Buryatsk ASSR; V.V. Timofeev, S. Ananshkin). These are peripheral points where the polecat is very rare and is very sporadically distributed. Thus, in Bauntovsk region, it occurs only in the upper course of the Tsipa in the region of Lake Okunevo in an area extending not more than 80–100 km along the river. The polecat occupies a similar, if not smaller, area along the upper Angara near the mouth of the Kuta (V.V. Timofeev).

In the east, beyond the Vitim, the northern border of the range sharply descends to the south and continues (Chitinsk district) across the upper Chita river (Pavlov, 1948), then turns to the east and across the middle course of the Nercha to reach the source of the Amazar (somewhat south of Mogocha at the [Siberian] railroad mainline). Thence, it steeply descends to the south to the Argun', nearly in the region of the mouth of the Gazimur, and exits beyond

⁵⁷Polecats were found at some points on the Ob' between the mouth of Tym (80° E. long.) and Surgut; *i.e.* north of 60° N. lat. were apparently, wrongly placed on Stroganov's map (1962)—these were not clarified in the text and contradict it. Old references (Kashchenko, 1900) to the distribution of polecats throughout the whole of "Tomsk Territory" are incorrect. North of Tomsk, the polecat does not pass beyond 57° N. lat. *i.e.* it occupies only the southern parts of Tomsk district.

the frontier (Favorskii, 1936; P. Zimin). Therefore, it is evident that the polecat does not reach the confluence of the Shilka and Argun', and contrary to the very widely distributed view, it does not occur in the upper reaches of the Amur.

A separate small area inhabited by the polecat in our country is located on the middle Amur. It occupies Blagoveshchensk region and the lower Zeya and extends eastward from Blagoveshchensk to Chesnokov (80 km to the east) and Poyarkov, apparently reaching the Bureya and occupies its lower [course] and, possibly, the foothills of Bureinsk range (Radde, 1862; Ogney, 1931, 1935; L.G. Turova). This section of the polecat range itself represents the northern edge of the region inhabited by the species in northeastern China (former Manchuria) and is connected with the Trans-Baikal region through this country. References to its occurrence along the Uda (Radde, 1862; Ognev, 1931; Stroganov, 1962) are apparently, mistaken. This error may be, at least partially, due to the fact that the data concerning the Uda—a tributary of the Selenga (Baikal basin)—where the Siberian polecat is common, were discounted because of the Uda, flowing into the Sea of Okhotsk

From the above-mentioned western point at Rava-Russkaya, the southern border of the range of the steppe polecat directs itself to the southeast, generally going along the Carpathians through L'vov and Stanislav, and farther envelops Chernovits from the north and east and somewhere in northern Moldavia, descends to the south and reaches the border of the USSR with Romania. Stepppe polecats are found throughout Moldavia (Kuznetsov, 1952) and in the region of the Danube mouth. In the Carpathians, this species is absent; only the black polecat lives there.

Farther to the east, the range extends southwards to the shores of the Black and Azov seas, and in the Crimea, the steppe polecat lives not only on the plains but also in the montane part, but apparently avoids thick forests and is absent on the southern shore.

In the Cis-Caucasus and Caucasus, the southern border of the range passes through the region a little south of Krasnodar along the foot of the northern slope through Nal'chik and Ordzhonikidze to Makhachkala on the Caspian Sea and thence descends to Derbent along the narrow coastal strip. In the west the border, approximately at the meridian of Gelendzhik, crosses the western spurs of the [Caucasus] range and the [species] range extends southeast as

a narrow strip along the shore itself nearly to Sukhumi. The polecat does not ascend the mountains (the foothills are wooded or were wooded) and is known to a height of only about 600 m (Psebai) or even less (Dinnik, 1914; Vereshchagin, 1947, 1959; V.G. Heptner). Therefore, in the Main Caucasus and in the Trans-Caucasus, the polecat is absent. In the regions adjacent to the northwest, north and northeast of the Caspian the range extends to the seacoast.

Precise borders of the steppe polecat range in Middle Asia still cannot be established. In any event, it is far from being distributed everywhere here, and the line of the southern border of the range in this country is quite complicated. The polecat exists both in Mangyshlak and on Buzach peninsula (Ognev, 1931; Gerbel'skii, 1939; Sludskii, 1953) and along the Caspian Sea (Kara-Bogaz-Gol; M. Laptev, 1936) the range descends to Krasnovodsk as a narrow extension and, perhaps, may go along the Sea and a little farther to the south, although data about this are very indefinite. In Bol'shoi Balkhan, the polecat is absent (V.G. Heptner, G.Sh. Shukurov).

From Krasnovodsk, the border of the range, passing north around Bol'shoi Balkhan, extends towards the northeast and, apparently, along Ustyurt Chink in which the polecat exists, particularly in its eastern part (Bazhanov, 1951) reaching the lower Amu-Dar'ya. In the delta and adjacent parts, polecats were noted in Muinak, Kungrad, Takhtakupyr and Khodzheil' regions. To the south, the polecat is distributed along the rivers, apparently, to Khiva and Urgench (Gladkov and Nikol'skii, 1935; Kostin, 1959; Ishunin, 1961). The polecat is absent in all remaining areas of Middle Asia west of the Amu-Dar'ya, both in the Karakum and throughout the southern regions adjacent to Iran and Afghanistan despite several claims to the contrary (Bobrinskii, 1944 and others) (V.G. Heptner).

The data of the range of the polecat in the regions to the east of the Amu-Dar'ya are scarce and in part, not well defined. It exists in the northwest, directly adjacent to Amu-Darya delta, and in the northern part of the Kyzylkum desert—here in particular, in the regions along the Kuvandar'ya and Dzhanydar'ya [rivers] (Ishunin, 1961). In remaining part of the desert the polecat is, apparently, absent. No clear positive data exist and that available, partial and suggestive are not definitive (Kuznetsov, 1948; Sludskii, 1953).

Farther, polecats exist, though sporadically distributed apparently, along the entire mountain system of the Tien Shan and in part, the Pamir-Alai. In the north, they are known in Dzhungarsk, Kirghizsk and Talassk ranges and in Karatau, and extend southward to the Alaisk valley. They are, however, absent in the Pamir (Rozanov, 1935; Flerov, 1935; Meklenburtsev, 1936). In the west, in Trans-Amu-Dar'ya part of Middle Asia, their occurrence was described between Chiili and Chimkent (Ogney, 1931), near Chinaz on the Syr-Dar'ya and in Dzhizaksk Golodnaya steppe (Sardoba; Ogney, 1931; Obruchevo station in Za-aminsk region; T.A. Pavlenko), on the left bank of Syr-Dar'ya in Begouat region (east of Dzhizak), in Khavast region in the foothills of the Turkestansk range and in Samarkand and Bukhara oases (Shafrikan, 50 km to the northeast of Bukhara). Farther south, the polecat is known in the Karsha, Guzar (southeast of Karsha) and Saryassii (near Denau at Surkhandar'ya) regions (Salikhbaev, 1939; Dubinin, 1954; Meklenburtsov, 1958; Ishunin, 1961; T.A. Pavlenko; V.G. Heptner). Farther south and east, references to this species are absent (Chernyshev, 1958).

Based on these places of occurrence, the border of the polecat range in the Trans-Amu-Dar'ya part of Middle Asia can be, apparently, preliminarily be given thusly. From the lower Amu-Dar'ya, probably at the level of Khiva or somewhat below, the border line includes parts of the desert directly adjacent to the delta (in particular, regions of old cultivation) and then turns northeast, continuing along those parts directed towards the Aral Sea, and crossing the Dzhandar'ya and Kuvandar'ya districts, reaches the Syr-Dar'ya, probably, somewhere in the Kzyl-orda district. Being directed towards Syr-Dar'ya or along this river, the border passes farther south, including the Golodnaya Steppe (at Dzhizak). Thence, it goes west along the Turkestansk range, probably south of Nuratau, where the polecat was not recorded (Meklenburtsev, 1937), and includes the oases along the Zeravshan as far as Bukhara.

Apparently, from somewhere in the region between Samarkand and Bukhara, the border passes at first southward to Karsha, then turning southeast, it envelops the Baisun mountains (in Kugitangtau polecat is, apparently, absent) and farther, moving eastward, goes on to Surkhandar'ya. Thence, in a still completely unclear form, it goes eastward across the Alaisk valley and exits to China. To the east of Surkhandar'ya, the polecat was not recorded (Chernyshev,

1958). According to some data (Sludskii, 1953, map), the polecat occupies the whole Kzylkum, which is, however, evidently incorrect (T.Z. Zakhidov).

Unique in the sense of its general outline, the range of the species and, to a considerable degree, its sporadic distribution in Middle Asia are determined by the fact that it avoids sandy deserts and in this country is a species to a great degree associated with the mountains and foothills, high montane valleys (Alaisk), and in part with the elevated areas in the plains. The sporadic distribution of the species is associated, probably, in addition to biotopic conditions, with some of our mountainous regions which the polecat may have penetrated from the east (Alaisk valley).

In the whole expanse from the Alaisk valley to the lower Argun' in Trans-Baikal, the range of the steppe polecat extends south beyond the border of the USSR. The high montane areas of the Altai and Sayan may constitute an exception, of which data, however, do not exist.

The range of the white polecat has noticeably broadened westwards in the last century, and in part northward. However, the chronology of its movement was poorly traced. In Tatariya, even 100 years ago it was not present, evidently, and even in the beginning of the XIX century it was believed that it was absent along the western side of the Ural range (Eversmann, 1850). At the end of the 60's (1866–1869), M.N. Bogdanov did not record the white polecat in the "chernozem belt of the Povolzh'e" (former Simbirsk, Kazan, and Saratov governances, the eastern part of Penzensk and western Ufimsk), though it is not excluded that he did not always differentiate between the two species (he also did not refer to the white polecat for the lower Volga).

At the beginning of the 90's of the previous century, the white polecat already inhabited all of former Saratov governance and in the beginning of our century penetrated into Tatariya but did not still occupy it entirely. Near Kazan, it appeared at the end of the 20's, and this was the most northerly point of occurrence of the species known at that time (Ognev, 1931). In the Omutninsk region of Kirov district the polecat apparently penetrated in the 40's of our century. If these indications perhaps do not completely accurately describe the chronology of movement of this species to the west and north in the Trans-Volga, in any event it can be considered that the tempo of its colonization is high.

In middle Russia, its colonization northward also was local, but the data concerning this, particularly on the penetration of the polecat to the Oka, are insufficient and are not accurate (see above, comparison of points of occurrence in expanse between Dnepr and Volga). In Vladimir district, where the described species do not represent a rarity (in 1960, 202 skins were prepared), it apparently appeared only at the end of the 30's—beginning of the 40's, however it had reached the northernmost regions (N.D. Sysoev). Judging by the fact that it is absent in some of the westernmost parts of the district (see above) and in Moscow district, it is not excluded that its settling proceeds not only from the south but in part from the east.

It apparently occupied Chernigovsk district mainly after the 20's. In Ternopol'sk and L'vov districts, white polecats appeared apparently, in the 40's of our century (first found in 1950). The stimulus for the colonization of the polecat here towards the west was, apparently, the appearance of settlements of European ground squirrels [Spermophilus suslicus] in this direction (Tatarinov, 1956).

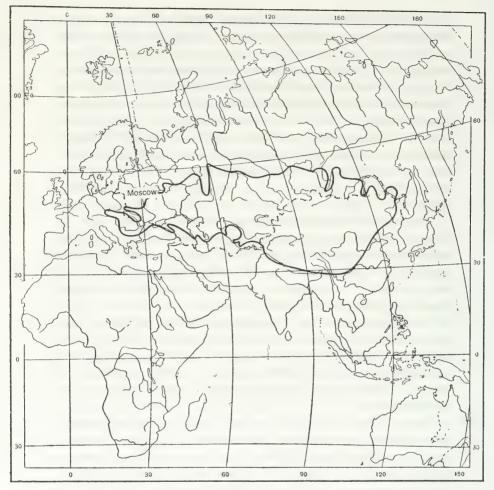
The appearance of the steppe polecat in Central Europe is also associated with recent times: in 1928 it was established in Hungary (Ehik, 1928), after several years in Trans-Carpathia, in 1948 in Czechoslovakia and in 1952-in Austria where it rapidly spread and its number strongly increased (Bauer, 1952; Kratochvil, 1962; O. Wettstein)58.

768 It is difficult to establish the time when the polecat generally began to move from Asia and settle in Europe. It went, apparently, mainly to the west along the south and as a secondary process from the south to the north. The latter movement, as was shown, is a phenomenon of our day and the last century.

It is possible that its movement along the most southerly route, at least in some parts, began also in the recent past, some hundred years ago. Concerning all of this, Pleistocene fossils of polecat (M. ev. soergeli) are known from France, Baden, Württemberg, Hungary and Austria and the Pleistocene and Holocene from the south-

ern European part of the USSR (Ekhik, 1928; Pidoplichko, 1951).

⁵⁸In light of the stated facts, information on the occurrence of steppe polecat near Warsaw (apparently in the last century; Ognev, 1931) is clearly wrong. It is possible that the capture of a chromist black polecat, the so-called "P. p. stantschinskii" was the basis for this mistake. Only a short time ago, the white polecat had slightly penetrated into Poland from Rava-Russkaya region.



768 Fig. 273. Species range of the white polecat, *Mustela (Putorius) eversmanni* Less. Southern and eastern borders in Asia to a considerable degree given provisionally. V.G. Heptner.

Nevertheless, the present polecats of central Europe must not be considered as autochthons. Obviously, the entire phenomenon, taken on a large scale, must be considered as a secondary reoccupation of the previous, for some reason abandon range.

If it is now difficult to say anything about the time of the appearance of the polecat in the southeast and the extreme south, and in part in central Europe, then, in any event the movement of the northern, western and southwestern borders in recent times are without doubt. It may be partially defined as the settlement of the

769 forest-steppe. The fact that the range of the steppe polecat in Europe is not yet completely formed is indicated by its very outlines, which do not completely correspond to the distribution of the natural landscapes.

Some expansion of the range to the north is occurring locally also in western Siberia; however, the progressive movement of the border there is very slow. In Siberia, colonization of polecat in new places is, apparently, directly associated with the cutting down and clearing of the taiga. In Europe, this cause also has certain significance (Trans-Kama); however, in many places, colonization of the polecat in many places is, apparently, determined by other, apparently partially internal reasons. This is very obvious in the forest-steppe and particularly in old cultivated regions in the extreme west of the range, where conditions of existence have not changed for a long time.

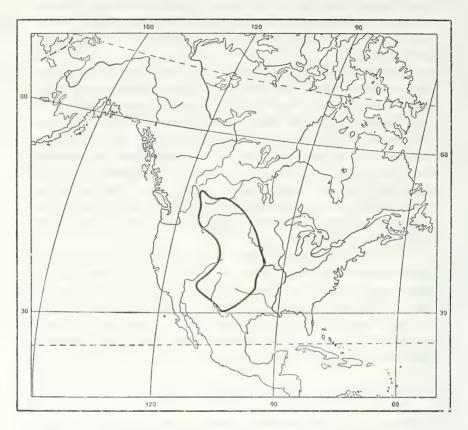
The sporadic distribution of the polecat in Cis-Baikaliya and Trans-Baikaliya among separate isolated small steppe areas (Lena, upper Angara and others) permits one to think, on the contrary, that the distribution of this species in Pribaikal was never large.

For the sake of accelerating colonization in Siberia, some attempts were made to acclimatize the polecat somewhat more to the north of the border of its natural range (Narymsk district; Lavroy, 1946).

Geographic Range outside the Soviet Union

In Europe, it occupies Romania (apparently, except montane wooded parts of the Carpathians), Hungary, western (Lower) Austria, Czechoslovakia, northern Bulgaria and northeastern Yugoslavia (Serbia).

In Asia, the range occupies Dzhungaria, the Mongolian Republic, Kashmir and Ladakh; in China—Tibet and the eastern part of the country from former Manchuria (except eastern) in the north to Sichuan in the south, including parts of Inner Mongolia. The 770 polecat is absent in the Korean Peninsula. In this expanse in Asia, the range has, apparently, large lacunae for example, in the northern taiga parts of the Mongolian Republic, they are mainly in the vast deserts, and perhaps in high montane regions of Tibet. Generally, the range in Asia outside the borders of the USSR is very poorly known.



769 Fig. 274. Range of the American form of steppe polecat [black-footed ferret], *Mustela* (*Putorius*) nigripes Aud. et Bachm. (from Hall and Kelson, 1959, simplified).

A closely related form, perhaps only a subspecies of our steppe polecat (see above), *M.* (*P.*) nigripes Audub. et Bachin, inhabits North America, occupying a very small range located in an irregular strip from southern Alberta and Saskatchewan in the north to Oklahoma, northern Texas and New Mexico in the south. It is very infrequent, apparently, endangered (extirpated), relict form (V.H.).

Geographic Variation

Despite the vast range, geographic variation of the white polecat is, relatively, not as great as might have been expected, especially taking into consideration that the animal is met with in very different natural regions. It is possible, that part of this is explained by the relatively recent colonization of the species in the western and most northern parts of its range (see above). Thus, it is noteworthy that variation is greater in the eastern and southeastern half of the range.

In a morphological sense, geographic variation is of small amplitude. The differences lie in changes in general color (degree of paleness of underfur, purity of dark color of the guard hairs and degree of their development, and degree of development of ocherous and red tones) and the color of separate parts of the body (head, neck), different density and length of fur, color contrasts, development (length) of the dark tail tip, and in part, in general dimensions (see above "Description" section and later).

Until a short time ago, geographic variation of our polecats, and also polecats of China and the Mongolian Republic was very little studied (for the fauna of the USSR, only Ognev, 1931) and in part, particularly, but unsatisfactorily, Central Asiatic polecats (Pocock, 1936). Relatively few forms were, however, described, and some of those were assigned to other species sometimes ("P. larvatus"); several from the very beginning were clearly unfounded. In 30's 3 forms were recognized (Ognev, 1931) in our fauna (5 were described), and for the entire species—5 (Pocock, 1936, including the form aureus). In recent years, a new revision of geographic variation of the polecats of Siberia and, in part, Kazakhstan (Stroganov, 1958, 1960, 1962) led to the description of 5 new subspecies, part of the time in obvious agreement with fur grades. Therefore, a system of nine races was formed only for Siberia (Stroganov, 1962) and of not less than 12 for the whole country.

Characters of this series of Siberian forms were based on times extremely subtle differences, hardly perceptible in a series of animals or even undetectable.⁵⁹

The number of recognized forms is, obviously, too great and gives an erroneous and exaggerated impression of geographic variation of the species. Even the number of the recognized fur grades is considered to be too large (Kuznetsov, 1952).

A full revision of geographic variation of the species is necessary.

⁵⁹The color plates in the work of Stroganov (1962) are technically so badly prepared that they cannot represent the individual color characteristics of the described forms and may be completely distort them. Compare, for example, illustrations and descriptions of the forms *lineiventer* and *tuvinicus*.

The enumeration below must be viewed as completely preliminary, of designated forms, in part good and in part weak. Among them, three groups are more or less clearly recognized: 1) polecats of Europe, western Siberia and northern part of Kazakhstan—group hungarica-eversmanni; 2) polecats of Trans-Baikaliya and Pri-Baikaliya, Mongolian Republic, Altai, mountains of Middle Asia and Tibet—group michnoi-larvata; perhaps the less known polecats of the plains of Middle Asia and southern Kazakhstan ("talassica") may be related to this group, but more probably they belong to the first group; 3) polecats of Priamur'e and the eastern part of former Manchuria—amurensis.

1. European steppe polecat, M. (P.) ev. hungarica Ehik, 1928 (syn. occidentalis).

Dimensions small. Pelage sparse and coarse. Color relatively dark-brownish, underfur yellowish, strongly darkened by the dark-tawny tips of guard hairs. Neck grayish-yellow, tail half sandy color, half dark-brown.

On the whole, color darker than in nominal form and other races.

Information on dimensions absent.

Westernmost part of range in European part of country, northwards apparently, to northern limit of distribution, eastwards, probably to Volga and northern Caucasus.

Outside the USSR—in Czechoslovakia, Austria, Hungary, northeastern Yugoslavia, northern Bulgaria, Romania and apparently in a small section of Poland at its boundary with L'vov district.

There has been no direct comparison of materials from southern Russian polecats, described as *occidentalis*, with those of Central Europe; however, their diagnoses are actually identical, and they must, apparently, be considered identical. The possibility is not excluded that the range of this form in our country is restricted to only the Trans-Carpathian plains. Polecats of the eastern parts of the Russian plains and the Cis-Urals have not been analyzed from the systematic side (see description of following form). Furriers assign animals from Astrakhan and Gur'ev districts to the "Russian grade", which evidently coincide with the described form.

2. Petropavlov [steppe] polecat, M. (P.) ev. eversmanni Lichtenstein, 1827 (syn. nobilis, pallida, heptapotamica, aurea).

Dimensions moderate. Winter pelage dense and soft, of moderate length. Length of guard hairs 32–35 mm or 35–38 mm. General color tone pale, straw-whitish, sometimes with ocherous tinge; underfur white or slightly yellowish-straw, sometimes pure white. Apices of guard hairs pure black ("pitch black"), black-brown or brown. Guard hairs on posterior part of back almost fail to darken the basic light color tone or darken it a little. Neck whitish. Tail not heavily furred, its basal part mainly whitish, the distal third black-brown.

Body length of males is 320–460 mm, females, 280–410; tail length of males is 80–160 mm, females, 70–140 mm; length of hind legs of males is 40–70 mm, females, 30–54 mm (after Zverev, 1931 and Stroganov, 1962).

Average dimensions (after Zverev, 1931): body length of males (561) 390 mm; females (671) 340 mm; tail length of males (519) 120 mm, females (528) 110 mm; length of hind leg of males (566) 50 mm, females (664) 40 mm (material from southeastern part of western Siberia—former Omsk and Slavgorod areas).

Condylobasal length of male skull is 61.7–71.3 mm, females, 52.4–61.3 mm; zygomatic width of males is 30.0–47.0 mm, females, 30.0–40.0 mm; mastoid width of males is 35.7–40.0 mm, females, 30.0–35.2 mm; interorbital width of males is 16.8–20.2 mm, females, 14.0–17.2 mm; postorbital width of males is 12.0–16.6 mm, females, 11.3–15.2 mm (skull measurements after Stroganov, 1962; data of nominal and three other forms are combined, excepting *aurea*).

In Trans-Volzh'e, western Siberia east to Cis-Baikaliya (Irkutsk district) and south to the Cis-Altai steppes, Pri-Balkhash, the plains portion of Semirech'e (Alma-Atinsk district), and Kazakhstan, except the southern part.

Outside the USSR [its occurrence has] not been established. It may possibly be encountered that part of China contiguous with eastern Kazakhstan.

In different parts of its range, this form exhibits certain deviations, for instance, in intensity of color of guard hairs, and their density; however, these populations hardly require separation into separate races, although several have been separated. In Trans-Volzh'e, the described form evidently transgresses into the European—in Trans-Volzh'e polecats, for instance, the black tip occupies half the length of the tail, and the skin is quite darkened

772

by the guard hairs. The limit of the range in the east is also poorly defined.

The form "P. p. aureus" Pocock, 1936 described from near Kazan, is not generally recognized, not only because of considerations previously given, but also because this form is apparently based on a hybrid specimen (see above).

3. Turkestan steppe polecat, M. (P.) ev. talassica Ognev, 1928.

Dimensions small. Winter fur long and dense, but somewhat coarse. General color very pale, whitish, without rusty tones; underfur slightly yellowish, guard hairs pitch-black, but length of black zone of guard hairs insignificant, so as to give a generally pale color. Head whitish, and mask hardly noticeable, neck almost white. Tail relatively heavily furred, basal part whitish, distal darkbrown. Summer fur very pale, without reddish tones, dark ends of guard hairs weakly defined, and mask very pale.

Data on dimensions are absent.

Southern edge of range of species, in area between Caspian Sea and [Lake] Balkhash—the western borders of Tien Shan (Talassk Alatau), southern Kazakhstan, Uzbekistan, Tadzhikistan and Turkmenia.

Absent outside the USSR.

A very little known form, apparently occupying the plains of Middle Asia and the southern belt of Kazakhstan, not penetrating high into the mountains. It is, possibly, related to the group of Central Asian races (*michnoi—larvata*; Ognev, 1931); however, it is evidently smaller and apparently is allied with those described above.

In the fastness of the Pamiro-Alatisk system (Alaisk valley), and possibly deep in the Tien Shan another form exists (see later) in several respects, perhaps close to this form.

4. Baikal steppe polecat, M. (P.) ev. michnoi Kastschenko, 1910 (syn. sibiricus, lineiventer, tuvinicus, dauricus).

Dimensions very large. Winter fur very long, somewhat coarse, with long shaggy guard hairs and sparse underfur. Length of guard hairs 64–68 mm, in posterior part of back, individual ones even longer (up to 80 mm). Tail densely furred with coarse hairs, its terminal third black. General color pale, whitish, with a black guard hairs, sometimes with light reddish tinge. This is determined by color of guard hairs, which are whitish at their bases and darkbrown or black at their tips and in the intermediate part, light

reddish-tawny. Yellowish-brown tint is more distinct on neck, shoulders and back. Contrast between light underfur and long black guard hairs creates sharply bicolored fur. Dark areas between the fore- and hind limbs are aften united by a narrow dark band extending along the middle of the abdomen. Summer fur (Trans-Baikaliya) is very bright, rusty-reddish that depends upon the complete or almost complete absence of black color in guard hairs and brightness of underfur, which is comparatively long.

Body length of males is 435–562 mm, females, 362–520 mm; tail length of males is 130–185 mm, females, 124–173 mm; length of hind foot of males is 54–80 mm, females, 48–72 mm; ear length of males is 24.5–26.5 mm, females, 23.5–26.0 mm.

Condylobasal length of male skull is 64.6–82.2 mm, females, 63.0–76.7 mm; zygomatic width of males is 37.3–58.9 mm, females, 36.9–48.7 mm; mastoid width of males is 35.7–47.9 mm, females, 35.3–43.2 mm; interorbital width of males is 16.2–24.2 mm; females, 16.6–19.4 mm; postorbital width of males is 12.0–773 17.0 mm, females, 12.0–18.0 mm (measurement from Stroganov, 1962; combined data of forms called by a number of synonyms).

Cis-Baikaliya on the west to the range of the form *eversmanni* [in the east], Trans-Baikaliya, Tuva, montane parts of Altai especially the south (Chuisk steppe).

Outside the USSR—western part of northeastern China (former Manchuria), Mongolian Republic and possibly the northern parts of Inner Mongolia and some (eastern) parts of Dzhungaria.

In some places, the described form may show several deviations in color and measurements; however, really convincing data about this are lacking. It is possible that some populations have transitional characters with other forms. Thus, perhaps that is the way things stand in the northern parts of Trans-Baikaliya, where it was shown comparatively (Stroganov, 1962) that color of polecats living there represents a transition to the form *amurensis*. At the same time, to recognize, as was assumed by Stroganov (1962), the presence of four independent races of polecat in that region, has no foundation. The features recorded for them are too indefinite and subtle and the ranges are too small for a predator of that type.

5. Tibetan steppe polecat, M. (P.) ev. larvata Hodgson*, 1849. Dimensions very large. Color light—underfur almost white, guard hairs black in color, but quite sparse. Red color tones absent.

^{*}In original text, misspelled "Hodgon"— Sci. Ed.

There are no data about body dimensions. Condylobasal length of male skull is 75 mm, and apparently even more, and female is up to 70 mm and may be more (material of Z[oological] M[useum of] M[oscow] U[niversity]).

In Alai valley.

Outside the USSR—in Tibet, Himalayas, Kashmir and, apparently, montane parts of Kashgaria.

This form is very little known both as regards its characteristics and also its distribution. It belongs to the group of large races of innermost Asia, in particular *michnoi*. To this latter it is undoubtedly close. It is possible that polecats deep in the eastern Tien Shan also belong to the Tibet form. Here [in this book], it is only conditionally recognized until there is a more complete revision of Central Asian polecats. It is possible that all polecats from Tibet through the Pamir-Alai, Tien Shan, Altai and Mongolian Republic to Pri-Baikaliya themselves (*michnoi*) represent one form.

6. Amur steppe polecat, M. (P.) ev. amurensis Ognev, 1930.

Dimensions moderate, apparently less than in preceding form. Pelage is short, of equal length over the entire skin very dense and soft, with guard hairs appearing only slightly above underfur. Length of guard hairs about 20 mm. General color of dorsal side bright reddish-ocherous, almost without dark tones in the posterior part, or brownish-reddish both on back and sides. Tail weakly furred reddish-yellow color through almost its whole length. Dark tip very short—about 32–36 mm against 60 mm and more in other forms, and has a brownish color.

Body length of males (5) is 340-410 mm; tail length is 100-140 mm; length of hind foot is 49-58 mm; length of ear is 22-28 mm.

Condylobasal length of male skull (4) is 64.1–66.4 mm; zygomatic width is 23.5–24.4 mm; interorbital width is 19.3–20.1 mm. Weight of males (5) is 575–800 gm (material from northeastern China; Shou, 1958).

On left bank of middle Amur.

Outside the USSR—eastern part of former Manchuria, and possibly farther south.

The Amur polecat itself comprises a well distinguished race. Against the general background of geographic variation of the species, it separates itself most sharply from all others. This applies both to general color tone of fur, also to difference in tail color;

and to very characteristic structure of winter fur. Although as pointed out, some characteristics of this form are revealed in gen774 eral fur tone of animals from Trans-Baikaliya, the Amur polecat differentiates itself from all other races or groups of races. It may be considered a representative of its own group of races. In this, it is, apparently the only form.

* * *

Steppe polecats living outside borders of our country have been very poorly studied, and their independence needs confirmation for both their morphology and distribution. Usually, the following forms are recognized: 1) M. (P.) ev. tiarata Hollister, 1913—Inner Mongolia, Gansu, Shaanxi, Sichuan; 2) M. (P.) ev. admirata Pocock, 1936–Chhili (Hebei), ? Shaanxi, Ordos. The form tiarata is close to michnoi but possibly still differs from it; the existence of admirata as an independent race is very doubtful.

The North American M. (P.) nigripes Audubon et Bachman may possibly belong to this species (see above) (V.H.).

Biology

Population. The steppe polecat is a common, locally an abundant predator; however, its populations are unevenly distributed, which is associated with the disposition of suitable habitats and their qualities, mainly with respect to abundance of principal foods. The polecat is particularly numerous where relatively large steppe rodents are abundant—ground squirrels and hamsters, etc.—and pikas.

For certain parts of the range, the density of inhabited burrows fluctuates within great limits; thus, in the Sal'sk steppes, density ranges from 8.3 to 1000.0 per 1000 hectares; in the Tersk steppes—from 5.0 to 40.0; in the Stavropol' steppes, more often 100.0 and up to 2000.0. In the Daurian steppes, the harvest of this animal in nine localities of 3 km² each was an average 45.0 per 1000 hectares, ranging from 14.0 to 113.0. For small individual sections, the concentration of inhabited burrows may reach 26 per hectare, taking into account the character of the colony (steppe ravines) (Sviridenko, 1935; Yurgenson, 1948). In western Siberia, characteristic density is 10 burrows per 1000 hectares; for former

Nizhne-Volzhsk territory-about 3.6. The steppe polecat is most numerous in the Cis-Caucasus and the Kazakhstan steppes between latitudes 48°-52° N. lat.

Figures for fur tanning are generally representative of the populations of this species in the USSR: in the pre-revolutionary years, the average annual harvest was about 900 thousand individuals. During 1924/25-1929/30, it fluctuated from 464 thousand to 1,296 thousand individuals. The yield per 1000 hectares for the whole range averaged 0.79, for the former North Caucasus territory-4.1, for Kazakhstan-1.56, and for former Nizhne-Volzhsk territory-0.87.

Habitat. The steppe polecat everywhere prefers open habitats level and foothill stepppes, fallow fields, pastures, slopes of meadows and ravines, and semideserts. It rarely inhabits cultivated areas, alpine and water meadows, herbaceous forest openings, and sections of desert landscapes covered by saxaul forests. In winter, it readily visits the frozen banks of steppe rivers and lakes. "In each case, the ecological setting in which the steppe polecat lives will correspond to that inhabited by one or another of those rodents species constituting its food objects, and therfore it is difficult to describe—it is variable" (Sviridenko, 1935). The steppe polecat ascends mountains to an altitude of 1860 m in the northern Caucasus, and to heights of 2000-2200 m in the mountains of Kazakhstan.

Food. The steppe polecat is a typical carnivorous animal. The polecat cannot assimilate plant food and it is absent in the diet (Zverev, 1931). Invertebrates are encountered rarely in summer foods, and only in individual sections of the range.

In contrast to the forest polecat, in the steppe polecat diet not 775 mouse-like rodents but the larger steppe rodents: ground squirrels, hamsters, pikas and others, are of decisive significance. Structural characteristics of its masticatory system (see above) is associated with this. Polecats cannot deal with such large rodents as adult marmots and they only feed on the young and injured animals and on dead bodies.

The best conditions for polecats occur in those places densely inhabited by ground squirrels. In these cases it feeds on them almost throughout the year, in warm periods seeking them on the surface and in autumn excavating their burrows, which the polecat does easily and quickly. Young polecats and females often enter

the burrows of ground squirrels without widening the passages. In steppes where ground squirrels are few or are completely absent, they are replaced by hamsters or pikas in the steppe polecat diet, or on the banks of water bodies, by water voles. In some places (separate regions of western Siberia and Trans-Baikaliya), consumption of ground squirrels bears a strictly seasonal character (Velizhanin, 1931). The close connection of the steppe polecat with ground squirrels is reflected by the distribution of its numbers, density, and in the character of daily and seasonal activity, absence of stable settlement, etc. Mouse-like rodents—mainly the various species of gray voles [Microtus] and hamsters—play the role of permanent substitute food—in winter in some parts of the range and in others—in times of depression in numbers of large rodents.

Fish, domestic fowl and carrion become of some significance for the polecat along the shores of rivers and lakes, or with insufficient regular foods. Birds are of secondary importance in the food of the steppe polecat. Among harvested birds, it attacks gray partridge [Perdix sp.] and willow grouse [Lagopus lagopus], but rarely grouse. Amphibians and reptiles do not occur often in its food, and not everywhere.

Geographical (see Table 69) and stand-type variation in foods of polecat are well marked. In Kazakhstan (Sludskii, 1953), in alpine meadows and in the mountains, it feeds on montane voles [Alticola], relict [S. relictus] and long-tailed ground squirrels [S. undulatus] and marmots, in forests—on hamsters, small voles and wood mice in sandy regions—on great gerbils [Rhombomys opimus], etc.

Even primary foods (occurrence not less than 14–16%) cannot be considered significantly stable in its winter diet. Over eight winter seasons in Volga-Kama territory (Grigor'ev and Teplov, 1939), voles were annually found in food analysis, water voles only in four seasons, and ground squirrels and hamsters, fish and amphibians in various combinations were encountered in only two seasons out of eight (each). This is associated with fluctuations in abundance of these groups of food resources in nature (Grigor'ev and Teplov, 1939).

In captivity, adult polecats ate 55–150 gm of food daily, on average—90.6 gm, and when fed only on beef they ate an average of 165.8 gm. Young polecat at age seven months ate an average of 145.5 gm daily and at the age of 2.5 months—155 gm. When fed ground squirrels, the daily requirement declined to 131 gm. Young

775 Table 69. Geographic and seasonal variation in foods of steppe polecat (% occurrence; Grigor'ev and Teplov, 1939; Kozlov, 1931; Zverev and Klimov, 1931; Sludskii, 1953; Fetisov, 1936; Brom et al., 1948)

Type of food	territory		Nizhne- Volga territory	Northern Kazakhstan	Western Siberia		
	Winter	Summer	Winter	Winter	Winter	Winter	Summer
Marmot	_	_		_	_	0.26	13.2
Ground squirrel	3.86	47.0	_	76.3	1.49	1.04	13.2
Hamster	5.69	47.1			23.3	_	-
Pika				_	_	76.2	15.4
Water vole	10.66		_	_	10.07		_
Great jerboa	0.92			6.8	2.45	0.26	2.2
Hamsters		_	_	5.2	9.8	4.32	4.4
Mouse-like rodents	59.4	52.9	12.5	6.8	31.3	13.6	4.4
Mole-voles [Ellobius]	0.36	_	_	2.6		_	-
Birds	7.53	4.9	7.4		1.7	3.0	2.2
Harvested birds	3.27	_	0.8		1.16	_	_
Common partridge	2.0	_	0.8	-	0.15	3.0	
Domestic fowl	0.73	_	5.8	_	_	_	_
Small birds	0.36		0.8	_	0.45		
Frogs	4.4	_			0.07		
Fish	5.5	_	29.1	_	0.22	_	_
Carrion	_	_	23.7	_	0.97	_	
Insects		_		_	-	_	12.2
Amount of data	550	103	118	38	1348	766	45

growing polecats, therefore, require more food than the adult per unit of live weight. Given 36 g of food, death due to starvation occurred on the 37th day, and on increasing the norm to 72 g, the polecat died on the 48th day. Therefore, the polecat eats in one day a quantity of food equaling 1/3 of its live weight; a norm of 1/6 its body weight does not maintain life functions. Young at the age of 30 days begin to tear at killed ground squirrels, though still nursing their mother. At the age of 40 days, they make independent attempts to kill ground squirrels, but unsuccessfully. After 10 more days, they can kill very young ground squirrels, but are not able to manage older ones (Sviridenko, 1935). According to other data (Zverev, 1931), steppe polecats in captivity eat from 70–250 gm per day.

Steppe polecats make food reserves that are often significant. In western Siberia, the following were found in burrows of steppe polecats: 1) 12 young ground squirrels; 2) 13 ground squirrels; 3) 5 ground squirrels; 4) 5 hamsters (Zverev, 1931). In Volga-Kama territory (Grigor'ev and Teplov, 1939), stores contained: 1) 4 vipers; 2) one hamster and 4 water voles; 3) 3 water voles and 2 gray voles. Probably, these stores that occur are not always utilized.

Home range. The steppe polecats do not belong among those animals with a sharply-defined home range. In the warm time of the year, especially in places rich in ground squirrels, old animals hold to a relatively settled mode of life until they destroy those found within an area a considerable distance from their burrows. They very quickly destroy ground squirrels within a radius 120 to 150 m from their burrows. Young polecats do not systematically attack all inhabited burrows of ground squirrels successively; they are more active, most often overnighting in the burrow of ground squirrel which they have eaten. Most settled are adult females nursing their litters. But even they, just after the young animals grow up, begin to roam together with the young animals (Sviridenko, 1935). Therefore, permanent home ranges are not well defined in steppe polecats and their outlines often change. The polecat lives in one home range for a few days up to 3-4 months.

With available food in abundance and shelters, the range of daily activity in summer is small. In winter, steppe polecat moves 12-18 km per day, often returning to the same burrow from which it set out to hunt. The area of daily activity was determined in one case as 3 km² (Zverev, 1931).

In winter, with worse conditions for capturing food, greater depth of snow cover, the animals move to areas more favorable to them. In such case, significant aggregations are sometimes formed, especially along the slopes of the steppe ravines or near settlements and Kazakh winter camps (Kazakhstan; V.G. Heptner).

Burrows and shelters. With rare exceptions, the steppe polecat does not independently dig its burrow, but uses those of steppe rodents—marmots, ground squirrels, hamsters, mole-voles, jerboas 777 and others, after slightly widening them. Due to this, internal construction of burrows occupied by steppe polecats, their dimensions, depth, number of entrances, etc. vary greatly (Sviridenko, 1935; Zverev, 1931). Moving frequently, they are little concerned about a well-constructed burrow. They adapt to the burrows of their prey, whose mode of life is similar to these predators. In

many cases, the burrow is only used once, sometimes for several days; and after that not visited for weeks.

Nesting burrows characteristically possess many outlets (from 3 to 15–20); moreover, alongside the nest chamber is a second chamber—for storing fresh food. Lining of the nest chamber does not occur. If one is present, it is the remains of the nest of the previous host. Characteristic signs of an inhabited burrow are presence of tracks, excrement, food remains and freshly thrown-out soil "shovelled" in 2–3 different directions. In burrows of males, the diameter of passages in hard soil is 9–12 cm, in female burrows—7–8 cm (in ground squirrels, 5–6 cm, rarely 7 cm). In soft soil, the diameter of passages is larger. Most often, polecats use descending passages of ground squirrel burrows, which are usually wider than vertical ones. Independently dug burrows are usually shallow and simple—they are used most often as temporary shelters in places where existing shelters are absent.

Daily activity and behavior. The steppe polecat has no sharply-defined rhythm of daily activity. It is mainly a crepuscular-nocturnal animal, active most of all at twilight and at dawn. Often, particularly in the warm time of year, it is met with during the day. Apparently, the short summer night is not sufficient for capturing food, especially for females nourishing large broods. Hunting by entire broods was observed during the day more than once.

The influence of weather on the activity of the steppe polecat has been professed, but is not strong. In winter, it is decreased at—30°C and lower. Daytime activity in summer is mainly observed in cloudy, not very hot weather and in winter, mainly during snowstorms or in foggy, cloudy weather. According to data from laboratory investigations (Kalabukhov, 1943), the rhythm of nocturnal activity in the steppe polecat is less well-defined than in the forest polecats. They are considerably more active in daylight hours. From 22 to 55% of all activity proceeds during the period from 0600 to 1800 hours (36.5% on the average against 17.9% in the black polecat). Females are more active at night than males.

The steppe polecat is an active, clever, brave and curious animal. It swims excellently and climbs well, but rarely use these abilities. They dig out the burrows of ground squirrels very rapidly. It catches its food in burrows and on the surface by waiting and hiding. While hunting ground squirrels, the polecat does not behave in a specific manner: after taking a certain direction, it

makes a great rush, often passing over inhabited burrows. While hunting, the polecat searches clefts, burrows and every object that attracts it, even if it is not experiencing hunger. In winter, when hunting mouse-like rodents, it makes numerous "plunges" under the snow (up to 18–20 in one hunt). Deep snow makes such means of catching food of little productivity, and the polecat is obliged to change its habitat to a less snowy one (Sviridenko, 1935).

Usually, the polecat moves in large leaps, and in places with an abundance of prey, it makes frequent loops. In contrast to other small predators which plunge under the snow, it returns to the surface through the same "plunge hole" and not in another place. The polecat can overcome tetraonid birds in their snow roosts. It is only able to catch ducks injured by hunters.

In connection with feeding to a great degree on large steppe burrowing rodents, the steppe polecat, as told, highly elaborated mobility and frequent changes in its home range. This did not help to develop a well-defined reflex for protecting its home range. The steppe polecat almost alone among mustelines is nearly the only 778 species forming, with [prey] abundance and a high concentration of food, colonies of high density. This is assisted in that, under such conditions, broods of young polecats are often large, do not disperse for a long time, and hunt together in a quite small area. For this reason, young animals are observed with an absence of aggression towards animals similar to them.

Seasonal migrations and transgressions. Quickly destroying its food resources, and not experiencing lack of shelters, steppe polecats, as a measure of diminution of food in a given place, migrate to another region of rodent abundance, sometimes moving to completely different surroundings (Sviridenko, 1935). They do not live in one place for a long time, especially the young. It was also noted that steppe polecats colonized along the track of colonizing ground squirrels. Thus, in the former Sal'sk province on the left bank of the Sai river where the ground squirrels recently appeared, steppe polecats were not previously known (the same was recorded in the steppes of North America where the same relationship exists between them* and prairie dogs, Seton-Thompson, 1921). In 1948, in the Daurian steppes, an unusual concentration of adult steppe polecats was observed in separate places as a result of local migrations; in one case, 10 adult polecats were caught in a two-

^{*}Black-footed ferret (Mustela nigripes)—Sci. Ed.

week period in May in an area of 3 km²; in another case in the same area, 33 polecats were caught in one month, 14 of which were caught on three successive days. Winter weather leads to unfavorable conditions for obtaining food, causing such movements (deep snow, see above). In autumn, polecats move more than 20 km per day (Sludskii, 1953).

Reproduction. Among representatives of the mustelid family, polecats are characterized by the most primitive type of seasonal sexual cycle (Kler, 1941). The period of complete sexual dormancy lasts from September to January. In captivity, mating of steppe polecats was observed in the first third of March (Zverev, 1931) and at the end of the month (Sviridenko, 1935). In the Moscow zoo, mating (7 cases) was observed from 9 April to 9 June. External signs of estrus appeared on 12–13 March and developed for 2–3 weaks. Then, after mating, they gradually disappeared within 3–4 days (Krumina, 1934).

In western Siberia, the period of rut occurs in March. In the northern Caucasus, mass mating takes place from the beginning of February to the middle of March. Sexual activity of male polecats in Trans-Baikaliya was observed up to the end of May, and by the end of June their testes had decreased in size to about 0.5 cm. The act of mating lasts from 20 minutes to 3 hours. In the absence of productive mating, estrus is repeated as is also the case after death of a brood. In the latter case, it may be repeated for three successive pregnancies. Usually, it occurs only once, and the female does not nourish more than one brood in the course of a year.

Pregnancy lasts 36–42 days (L. Vakhrameeva), or 40–43 days (Krumina, 1934). In other experiments (Sviridenko, 1935) in three cases pregnancy lasted 36 days after the first mating. Placentation occurs after 14 days, of which the latent phase lasts 7–8 days (blastocyst stage; Kler, 1941).

The number of young in a litter is from 3-6 to 18. Average number from 33 cases recorded in the literature is 9.5.

Growth, development and molt. Steppe polecats are born blind, naked and pale rose. Ears are covered by a membrane. Body length is 6.5–7.0 cm, weight is 4.5 gm (Sviridenko, 1935). According to data of Moscow Zoo, the body length of newborns is 5–6 cm and body weight is 10 gm. These figures fluctuate depending on the number of young in the litter (Krumina, 1934).

After three days, a thin white underfur appears on the body surface. On the 9th day, the body length doubles and body weight increases six-fold (33 gm). At the same time, milk teeth begin to erupt and the feet are observed to darken. On the 20th day, the color darkens and typical difference in color of the muzzle appears. At that time, the young polecats weigh 70-72 gm. Teeth continue to erupt and color to darken. Eyes open on the 28th-34th 779 day. At that time, the polecats already crawl freely, lick blood, and even try to tear apart prey, although continuing to feed themselves on the mother's milk. Body length of a one-month polecat is 190 mm and its weight is 138 gm. At the age of 45 days, they can already themselves deal with young ground squirrels and at the age of 60 days—with adults. They live in the family burrow for 2-2.5 months. Dispersal begins from July, or later depending on time of delivery*. Young polecats living independently are already observed in September. Only the female takes care of the brood, but in a series of cases, participation of a male in feeding the brood was observed.

Polecats attain sexual maturity at 10 months, but complete development of the organism is reached only at the age of 2 years, when skull formation is completed.

The steppe polecat molts twice per year: in spring and in autumn.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The steppe polecat has many enemies: wolf, red fox, corsac fox, imperial eagle and snowy owl. However, their role in the population dynamics of the species is hardly significant.

Competitors of polecat include: solongoi, kolonok, weasel, ermine, forest polecat, manul, steppe [red] fox, and corsac fox, as well as all species of diurnal and nocturnal birds of prey living in open areas. In summer, the polecat coexists in contact with the majority of species of small carnivores, except for solongoi and weasel, only at the ecological borders of its distribution within the range.

Among infectious diseases, the polecat is weakly susceptible to rodent [sylvatic] plague, tularemia and viral disease—canine distemper. Only weak individuals are susceptible to pasteurellosis. Helminthic infections are widespread among polecats. Ticks strongly attack the steppe polecat. It is parasitized, often in great numbers,

^{*}Literally, "appearance in the light"-Sci. Ed.



779 Fig. 275. Paired footprints of steppe polecat while quickly jumping on snow, and scheme of the track. Voronezh district, 8 January 1952. Sketch by A.N. Formozov, about 2/3's natural size.

by more than 11 flea species, partly transmitted to polecats from rodents on which they feed.

There are no data on mortality.

Population fluctuations in steppe polecats are clearly evident. They are induced by food deficiency, epizootics and the death of both adult and young polecats as a result of steppe fires in dry years, unusually large flooding of steppes by snow-melt water in spring and also massive treatment of steppe lands with poisons for the struggle against harmful rodents (Sludskii, 1953; Zalesskii, 1931;

Sviridenko, 1935). In 1938, a catastrophic fall in number all over Kazakhstan was observed as a result of the severe ice storms in early spring which hindered hunting by polecats, and following which many rodents died (Sludskii, 1953).

In the steppes of southeastern Trans-Baikaliya, population fluctuation of the steppe polecat is well noted, but the range of fluctuations is less than that in other carnivorous animals in this region. In 1939–1948, these fluctuations were 11 times higher due to the very high rise in their number in 1939, which was associated with a rare abundance of the Daurian pika [Ochotona daurica] and groups of gregarious vole [Microtus socialis]*. From 1940 to 1948, changes in numbers were only four-fold. During these nine years, the changes in numbers of the steppe polecat were parallel to those of the long-legged buzzard [Buteo hemilasius] and almost coincided with changes in the numbers of Daurian pikas and narrow-skulled voles.

Field characteristics. It is not difficult to distinguish the steppe polecat in open habitats. Its tracks on snow, sand or dirt are well distinguished from tracks of solongoi, ermine and weasel by their larger size. Aid in determination of species attribution of the tracks may always be the habitat in which they occur, since in those where steppe polecat coexists with forest polecat or kolonok, they almost always occupy different habitats. The prints of claws and callosities of the soles of the steppe polecat are always very sharp; the length of its leap is 40–65 cm (Formozov, 1930). In moving, it often "trots" (P.Yu.).

Practical Significance

The significance of the steppe polecat to the national economy of the USSR is great. It is particularly valued as a destroyer of rodents harmful to agriculture, mainly ground squirrels. According to very minimal calculation, the steppe polecat can destroy no fewer than 200–300 ground squirrels per year, not counting mice and voles.⁶⁰

In regions where the steppe polecat feeds mainly on mouselike rodents, it can destroy about 1500 specimens in the winter alone (Sviridenko, 1935). In regions with weakly developed agriculture, the steppe polecat is very useful, destroying natural foci

^{*}The Russian word is "stadnykh"-Sci. Ed.

⁶⁰In an active season, one ground squirrel eats about 6 kg food, 25% of which consists of grains.

of disease transmitters and reservoirs where infections begin—ground squirrels and other steppe rodents.

The steppe polecat is very important for the fur trade of the USSR; in individual years, the price of its skins has occupied seventh place; in Kazakhstan and several other places, the steppe belt polecat occupies one of the first places. Its durable beautiful skin was always in demand in the national and international markets. However, in past years, from 1926-1929 to 1956-1959, the catch of steppe polecat noticeably decreased. Along the Cis-Caucasus, the catch decreased 4 times; in Bashkiria—6 times, in Middle Povolzh'e—10 times, in the republics of Middle Asia—14 times, and in Nizhnyi Povolzh'e—17 times (Danilov, 1936). Apparently, besides profound changes in the economy of the fur trade, a considerable role is also played by such factors as changes in steppe landscape and decrease in food resources (ground squirrels, hamsters and others) in connection with the application of chemical methods for control of rodents, with ploughing of virgin soil, and with changes in agrotechnical methods, etc.

Harvesting this animal is simple and profitable; it is mainly taken with jaw traps placed near the inhabited burrows. In the northern Caucasus, up to 100-150 were caught in one season using 10-16 jaw traps (Sviridenko, 1935), in Nizhnyi Volga—up to 60 polecats by one hunter.

The best method for maintaining the number of steppe polecats at the desired level, which is usually determined by the opposing interests of fur trade and agriculture, is periodic prohibition of its harvest for 2–3 years. The prohibition must include not less than a whole district or territory, otherwise, it will not be effective. In districts of field-protecting forest belts, it is necessary to prohibit completely the harvest of steppe polecat during the whole period of planting for the protection of the fields and the young seedlings from ground squirrels (P.Yu.).

Genus of Marbled Polecats

Genus Vormela Blasius, 1884

1884. Vormela. Blasius. Berichte d. Naturforsch. Ges. Bamberg, 13, p. 9. Mustela sarmatica Pallas = Mustela peregusna Gueldensta edt.

General dimensions small.

Skull small, relatively short and wide, in general appearance similar to skull of steppe polecat, *Mustela (Putorius) eversmanni*, but smaller than it. Protuberances, crests etc. of skull well developed—occipital well-defined, sagittal relatively weak, but quite pronounced, anteriorly bifurcating and giving off branches to postorbital processes. Brain case relatively small, not elongated, quite wide; zygomatic arches strong, quite sharply separated, only slightly wider than braincase in its widest place. Postorbital processes quite large and massive.

In postorbital region a sharp constriction is present—line of lateral borders of this part of skull begin to come together at an angle and then diverge again. Least width in region of postorbital constriction less than interorbital width. On the whole, this region is relatively short. Skull noticeably flattened. Line of upper profile of skull relatively straight. It is highest of all in occipital region and gradually declines anteriorly; elevation in interorbital region is weakly defined; line of upper profile in facial part not reduced sharply. Diameter of infraorbital foramen considerably smaller than canine alveolus.

Auditory bullae moderately swollen, somewhat angular (irregular triangular) in outline, only slightly more widely separated in posterior part than in anterior. On the whole, bullae seem to be displaced forward and their anterior edge nearly reaches to the foramen ovale, posterior ends of hook-like processes of pterygoid bones touch and are fused with anterior part of bullae. Mastoid (mammary) processes relatively weak, paroccipital (exoccipital) processes—well developed. Bony palate wide.

Dental formula
$$I = \frac{3}{3}C + \frac{1}{1}P + \frac{3}{3}M + \frac{1}{2} = 34$$
. Teeth are strong—rela-

tively a little stronger than in genus *Mustela*. Canines, especially upper, are longer. Main cusp of last lower premolar (third tooth behind canine—in front of carnassial) has no additional cusplets on inner side. Lower carnassial tooth bears small additional cusplet on inner side of main cusp. Upper carnassial tooth is strong—width of its cutting part approximately equal to half of its length. Upper molar (last in the series) has inner and outer sides of equal length, or inner side is slightly more massive—last tooth is not constricted appearing as two blades (inner and outer), or constriction is ill-defined.

Trunk thin and elongated, limbs short, tail relatively long (about half length of body plus head). Head small, blunt; ears large and broad. Anal scent glands present.

Fur relatively short and coarse, more or less even in length throughout the whole body; tail fluffy. Color entirely unique—bright and variegated, consisting of patches and areas of black, yellow and white colors. There is no distinctive light throat patch. On facial surface of the head, well-marked black-and-white mask.



782 Fig. 276. Reconstructed range of genus *Vormela Blas.*, and reconstructed range of marbled polecat, *Vormela peregusna* Gueld. V.G. Heptner.

A terrestrial animal, associated with open, arid, level areas and with burrows of mass settlement of rodent species (ground squirrels, gerbils). A specialized predator, feeding mainly on rodents.

Range of the genus relatively small and occupies southeastern Europe, parts of Asia Minor, Middle Asia, Kazakhstan, and northern parts of Central Asia (for details see following description of species range).

783 Genus is monotypic.

Genus Vormela is very well and strictly characterized, and of its independence no one raises any doubts. It long ago—evidently even in the Pliocene—constituted a group, with its origin probably in Asia Minor (fossils are known from the Pleistocene in Syria, Palestine and the Caucasus). In its systematic position, the genus apparently stands closest to the genus Mustela, namely, to that branch which includes the true polecats (subgenus Putorius). If one of its main features—its entirely peculiar color—is set to one side, it is most similar to the steppe polecat. Speaking essentially of skull structure, actual fundamental differences are only in structure of auditory bullae and their location relative to the pterygoid bones and the foramen ovale, and particularities of the dentition. In all remaining aspects, craniological differences between these two species are not greater, and in some respects, less, than those between several species of the genus Mustela. Even color, with all of its peculiarity, is similar to the color of polecats in some characteristics (dark venter, facial mask).

Genus Vormela has several features of similarity particularly in color, to different African forms of the family (Ictonyx, Poecilictis, Poecilogale). Attempts to closely affiliate the genera Vormela and Ictonyx (Pohle, 1933) did not meet with acceptance (Pocock, 1936), although between them there are some common craniological features (fusion of pterygoid processes with tympanic bullae). Equally with genus Mustela, but particularly subgenus Putorius, genus Vormela, as was shown earlier, reveals characters with proximity to the monotypic North African genus Poecilicitis (libyca; Zorilla libyca auct.) and is usually placed between them in the system. Sometimes, Vormela is considered more closely related to Poecilictis than to Putorius (Mensel, 1881). The whole question of generic groups closely related to Mustela requires special study.

In composition of fauna of the USSR there is one species: marbled polecat, *Vormela peregusna* Gueldenstaedt, 1770.

Found in steppes and deserts of southern European part of USSR, Causasus, Middle Asia, and Kazakhstan.

A fur-bearing species, also of significance as a regulator of numbers of several rodents, in particular reservoirs of harmful infections (V.H.).

MARBLED POLECAT, PEREVYAZKA¹

Vormela peregusna Güldenstaedt, 1770

- 1770. Mustela peregusna. Güldenstaedt. Novi Comm. Acad. Sc. Imp. Petrop., 14, 1, p. 441. Steppes along lower Don.
- 1771. Mustela sarmatica Pallas. Reise durch versch. Prov. d. Russ. Reiches. 1, p. 175, 453. Between Syzran' and Medveditsa river.
- 1910. Vormela koshevnikovi. Satunin. Zool. Anz., 36, p. 59. Ashkhabad.
- 1910. Vormela tedshcenica. Satunin. Zool. Anz., 36, p. 60. Tedzhensk oasis, Turkmeniya.
- 784 1910. Vormela sarmatica alpherakyi. Birula. Izhegodn. Zoolog. muzeya. Ak. Nauk, 15, p. 333. Near Ashkhabad.
 - 1910. Vormela negans. Miller. Proc. U.S. Nat. Mus., 38, p. 385, plate 17. Ordos desert, about 100 miles north of Yulinfu (Yuilin').
 - 1935. Vormela peregusna peregusna natio intermedia. Ognev. Zveri SSSR i pril. stran, 3, p. 70. Starogladovsk Station on Terek [river].
 - 1976. Vormela peregusna euxina. Pocock. Proc. Zool. Soc. London, p. 718. Malsosi, Dobrudzha, Romania.
 - 1936. Vormela peregusna syriaca. Pocock. Ibidem, p. 720. Tiberias* Lake, Syria.

¹Perevyazka—is now an artificial, bookish name, though in the 18th century, it was apparently in use in the Ukraine (Pallas, 1811). Perhaps it is connected with the striking white transverse band ("bandage") across the facial part. In the steppes of the northern Caucasus, in particular along the Terek (V.G. Heptner) and in Kuban' (Dinnik, 1914), the name "berguznaya" existed widely. The name given by Gueldenstaedt itself represents simply a Latinized Russian word. Long ago (18th century) among furriers and sometimes also now, the name "polecat-perevozchik" or simply "perevozchik" is used. This name is without meaning. It may itself represent a distortion of one of the old Ukrainian folk names "perevyznik" (Pallas, 1811).

*In Russian original, rendered as "Tiveriadsk"—Sci. Ed.

- 1936. Vormela peregusna ornata. Pocock. Ibidem, p. 721. Near Lake Baikal—Nomen delendum! (V.H.).
- 1948. Vormela peregusna pallidior. Stroganov. Tr. Zool. Inst. AN SSSR, 7, p. 129. Semirech'e, former Kopal'sk co.
- 1948. Vormela peregusna obscura. Stroganov. Ibidem, p. 131. Vakhsh valley, Tadzhikistan (V.H.).

Diagnosis

Only species in its genus.

Description

In general appearance, the marbled polecat is very similar to polecats. As in them, it often moves in leaps, usually arching the back. With this, however, several of its ecological particularities are noticeably different from polecats: instead of a sharp chirp, the voice is threatening—a peculiar growl or grumble, and adopts a special defensive pose, etc. (see below).

Head small and narrow, muzzle obviously blunt, ears relatively very large—tall and broad at base, sharply delineated due to their



784 Fig. 277. Marbled polecat Vormela peregusna Güld. Sketch by A.N. Komarov.



785 Fig. 278. Marbled polecat Vormela peregusna Güld. Badkhyz preserve, southern Turkmeniya. May 1962. Photograph by Yu.K. Gorelov.

coloration. Tail long, constituting about half of body length or slightly more, covered with long hairs, very fluffy.

Winter fur quite short and not very close-fitting, with relatively weakly developed underfur and dense guard hairs. Fur, not counting very long hairs on tail, is even, and sharp contrast between underfur and protruding guard hairs, as in polecats, is absent in marbled polecat. Winter fur quite soft. Summer fur somewhat shorter, sparser and coarser than winter [fur]*, but in general, differences in characteristics between winter and summer fur relatively small, and much less than in northern forms of subfamily, even, apparently, less than in steppe polecat.

Anal glands present. Teats 5 pairs (4 abdominal, 1 thoracic; Ognev, 1935).

Color of the marbled polecat is to the highest degree unique it is very variegated and itself consists of a combination of black, yellow and white areas and spots. It may be interpreted as a combination of facial pattern of the "mask" type (apparently, the extreme degree of development in the family) and a saddle-patch**

^{*}In Russian original, reads "summer," a lapsus—Sci. Ed.

^{**}In Russian, chebrak, from Turkic shabrak, or saddle blanket—Sci. Ed.

pattern. In general, it may be considered that it corresponds with that type of color which, within the family Mustelidae, is developed in honey-badgers, badgers and African polecats of the genera Poecilogale, Leptonyx* and Poecilictis, but purely morphologically, itself apparently represent an extreme degree of development and complication.

Color of the marbled polecat is not only complicated, but entirely variable individually and, to a lesser degree, geographically. In main features it may be represented by the following scheme (after A.A. Byalynitskii-Birula from Ogney, 1935, with modifications and additions) according to the four main color fields (Fig. 282)². Color of whole venter of body from throat to base of the tail, including lower part of sides and legs, shining black color with light brownish tints. Bases of hairs on belly are grayishbrownish. Sometimes in middle of posterior part of belly, small light-rusty dots occur, or several light spots are found.

Head color very clear and, contrasting, consisting of black and 786 pure white parts. Upper and lower lips, back to corners of mouth and chin—"peristomal ring"—pure white. Quite wide black stripe passes through eyes in form of transverse band. Descending to sides of head and reaching corners of mouth, it unites with black throat area. Behind this black band, a quite broad pure white transverse stripe runs between eyes and ears—"frontal band". On reaching lateral head surface of the head, it slopes somewhat posteriorly, passing below ear and ending on sides of ear. Remaining part of head behind white frontal belt, including occiput, black. Ears located on this black area. At the base and posteriorly they are black; edges support broad pure white margins of somewhat longer hairs. These bright ear margins make already large ears look even larger. Bare tip of nose black.

Upper side of neck dark, brownish-black with light pattern consisting of three fields-two laterally which are wide and a narrow middle one that widens anteriorly. Width of lateral stripe and degree of development moderately variable—it is sometimes broken into several spots. In some cases, anterior parts of all three neck stripes themselves united in transverse direction, thus forming another transverse, more or less wide, white stripe at base of

^{*}A synonym of Amblonyx, the African clawless otter, which lacks black and white coloration. Leptonyx is a lapsus, Ictonyx clearly being intended—Sci.

²Description given mainly after southern Russian form and schematically because of its great variability. For additions, see below, and section on "Geographic variation".

nape corresponding as it were, to frontal band. Together with lateral stripes (in these cases, the middle one is poorly defined), it forms an angular bracket-like figure opening posteriorly—"collar". Color of neck stripes white—somewhat yellowish in posterior part, and main tone of this part of neck brown or rusty-brown.

Whole dorsal side from shoulder region to base of tail or almost base, occupied by variegated saddle-patch. It spreads ventrally and laterally, especially in posterior half of body, where it also covers upper part of thigh. In anterior part, saddle-patch bordered laterally by two usually quite broad white or yellow, somewhat curved scapular stripes. They extend backward approximately to posterior border of thorax or somewhat farther. Directly, or through series of spots, they pass to analogous stripes bounding saddle-patch in its posterior part—thigh stripes. They have same color, but on the whole are much less defined than scapular ones. At base of tail, along flanks, lie two oblong, light anal* spots. They are quite variable in size; sometimes each of them is divided into two, or there is a connection between them.

The actual saddle-patch itself represents a large area of basically brown tone. Throughout it are scattered coarse yellow, sometimes very light spots of irregular form. Often these spots flow together in longitudinal direction and form small, quite variable stripes. Nearer to the edges of the saddle-patch and along the very edge, the tendency towards fusion of spots and formation of stripes is stronger, and here they often completely fuse with the thigh stripes, from whence the latter loses its definition.

The basic tone of the saddle-patch may also be yellow and in this case, relatively small, more or less rounded spots of brown color are scattered over it. They also sometimes display a tendency towards fusion into longitudinal, oblique, and even transverse groups. The anterior part of the saddle-patch is commonly more densely covered with spots; in its posterior portion they are smaller, more sparsely scattered, and the yellow field of the saddle-patch is paler, on the whole, more clearly defined and more striking to the eye.

Both described types of saddle-patch themselves represent negatives of one another—in saddle-patches with light main field, this field is formed by a strong increase in area and number of fused yellow spots, and the brownish spots on it are, apparently,

^{*}In the Russian original, "analnykh (poroshitsevykh)"; both words appear to have the same meaning—Sci. Ed.

the remains of the main dark background of saddle-patches of the first type. On the whole, saddle-patch color is to the highest degree variable, both in general features and details. From the color type in which all basic elements of the saddle-patch are expressed, are derived the origins of all forms; one side, as far as a large, light, area with insignificant dark spotting, and on the other hand—up to a dark dorsum with a relatively very small number of light spots. In the first case, thigh stripes completely disappear, while scapulars are poorly developed, and in the second, scapular stripes are very well expressed and thigh stripes are commonly sufficiently marked—they are continuous or broken into individual spots. Scapular stripes are usually well differentiated in all cases.

Base of tail is rusty-brownish or brown in color. Its middle—the longest part—is a pale-straw segment with brownish highlights, and the tip is bright blackish-brown. Color of individual hairs at their base and proximal part is pale-rusty-whitish, and distal part is rusty-brownish and bright. Base of hairs on middle part of tail whitish, passing farther to a brownish-rusty and in part brown band, and hair tip white or slightly yellow. Lower surface of tail at base region darker than upper, usually bright blackish-brown and on remaining part, as on upper side.

Vibrissae and hairs covering soles of feet dark-brown, foot pads not covered with hairs in winter. Claws light, quite long, weakly curved.

The above-described deviations in color do not comprise the whole range of its variability. Individual parts of pattern on head vary in color and form. The [white] peristomal ring occupies the chin to a variable extent (except for lips, it may be entirely black); the white frontal band may descend on the sides of the head and neck to a variable degree—sometimes ending below the ear, sometimes passing farther onto the throat, and in some cases, being interrupted on the forehead by black, in others uniting under the eye with the peristomal ring, etc. Sometimes, light spots appear on the middle of the abdomen as if uniting the saddle-patch edges from opposite sides. Finally, the intensity of color varies in both dark—black and brown—and light areas—yellow and pure white color.

All the changes mentioned are mainly of an individual character; however, in some characters geographic variation also reveals itself. This concerns general tone of saddle-patch and the relative

degree of development of dark and light tones of its basic background, sharpness of pattern of scapular and thigh stripes, general intensity of ventral black tone, appearance of light spots on abdomen, etc. Sharp mutational changes in color have not been described in the marbled polecat.

Sexual dimorphism in color is absent. Color of young differs from adult color, the elderly being more intense and darker in basic brown color of saddle-patch, its spotting being lighter with more noticeable development of yellow tone. The tail is less fluffy.

Seasonal variation in color is not expressed or is weak.

For characteristics of skull, see above in characteristics of the genus.

The structure of the os penis is in the main similar to majority of species in genus *Mustela* in particular, to the polecats. Its base is laterally compressed, and the distal third is bent upward hooklike. The dorsal surface of the basal half carries a rib-shaped elevation, and the end is flattened. The very tip itself forms a rounded denticle slightly bent to the right. There is no groove on the lower surface of the basal part, but terminally it is well-developed.

Dimensions of the marbled polecat are not subject to great individual variation; in particular, especially large individuals have not been noted.

Body length of males is 269–352 mm, of females, 290–345 mm; tail length of males is 118–205 mm, of females, 159–184 mm; length of hind foot of males is 39–50 mm, of females, 38–45 mm; ear length of males is 20.5–31.0 mm; of females 24–27 mm (from approximately 90 individuals, after Ognev, 1935; Pocock, 1936; Stroganov, 1948, 1962; Chernyshev, 1958 and material of the Z[oological] M[useum of] M[oscow] U[niversity]).

Condylobasal length of male skull is 50.6–62.0 mm, of females, 49.0–56.3 mm; zygomatic width of males is 29.9–39.0 mm, of females, 30.0–34.9 mm; interorbital width of males is 13.1–19.0 mm, of females, 13.1–16.0 mm; mastoid width of males is 26.1–32.6 mm, of females, 27.2–30.2 mm.

Os penis length is 36.9-39.2 mm (3 individuals; Ognev, 1935). General weight is 370-715 gm (V.H.).

78

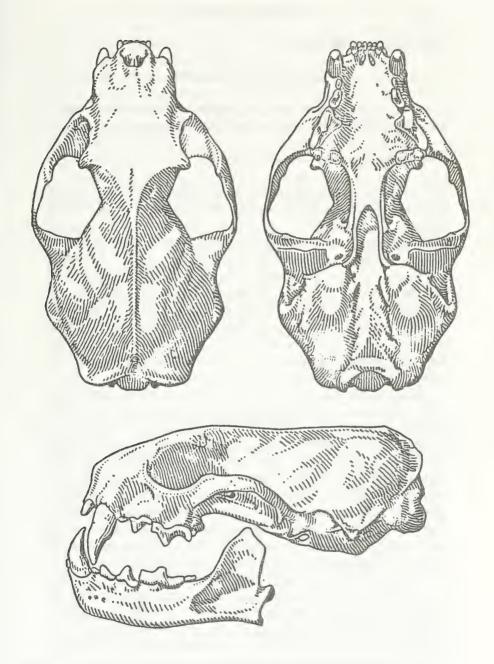


Fig. 279. Skull of marbled polecat, Vormela peregusna Güld.

Systematic Position

Only species in the genus.

Geographic Distribution

Found in steppes, semideserts and deserts of southeastern Europe, Near East, Middle Asia and part of Central Asia.

Geographic Range in the Soviet Union

The range (reconstructed) constitutes a considerable part of the range of the species and itself represents the north of its western half.

In the west, the northern boundary of the range begins at Belovezhsk Forest (approximately 53° N. lat. and 24° E. long.). Thence, it is directed to the southeast, to Kiev, and then rises again towards the north, reaching the Maloarkhangel'sk region (at the source of the Oka—52° 20′), is directed eastward to the Voronezh region (Voronezh preserve) and thence, in an imprecise way proceeds to the Volga—to Syzran' or a little south of Syzran'. Beyond the Volga the border, apparently, rises north of 52° [N. lat.] and directs itself to Orenburg on the Ural river.

South of this line, the range in the west extended, apparently, to the foot of the Carpathian mountains but in these mountains, the marbled polecat was evidently not present. It was also not recorded in the Trans-Carpathians. The range probably extended into Romania in the extreme lower Danube. Apparently, the marbled polecat existed all over Moldavia. Farther to the east, the range of the marbled polecat everywhere reaches the shores of the Black and Azov seas, occupies the Crimean steppes (marbled polecat is absent in montane Crimea, but was noted at Balaklava) and extends to the shore of the Caspian Sea. In the Caucasus, the marbled polecat is distributed over the entire Cis-Caucasus steppes from the mouth of the Kuban' to Makhachkala, reaching the foot of the mountains (Nal'chik, Vladikavkaz). In places, it goes up into the foothills somewhat (Psebai on the Belaya-a tributary of Kuban'), but in wooded montane regions, it goes no higher than 600-700 m above sea level. It is found along the entire Caspian shoreline to Derbent, and farther south, to Baku.

In the Trans-Caucasus, the marbled polecat inhabits the plains and foothills in the Kura and Araks basins, passing along the Kura to Tbilisi. In Armenia, it is met with along the valley of the Araks and the montane steppe region and in semideserts north of it, proceeding into the western part of the country (to the west of [Lake] Sevan) to Kirovakan region and Leninakan (latitude 40° 15' N. lat.) and somewhat north of it—to Gukasyan region (41° 00′ N. lat.). In this part of the Trans-Caucasus, the marbled polecat is found at a height of 1700 m. It is encountered in the Lenkoran depression and in unforested places of Talysh at heights up to 2000 m.

Beyond the Urals, the northern border of the range from Orenburg and the Ural river passes southeastwards to the upper Emba, and then swings to the east and, occupying the Pri-Aral'sk Karakum', is directed to the Ulutau mountains, to the upper Sarysu and Semipalatinsk. Thence, it enters into the Cis-Altai steppes and goes on to Rubtsovsk and Biisk. In the Biisk region, it swings sharply around to the southwest (the eastern end of the range forms a sharp extension) goes along the Altai foothills including Ust'-Kamenogorsk region and Katon-Karagai, and the Zaisan depression, and here exits beyond the borders of our country to Dzhungaria [Chinal.

To the south of the above-mentioned line, in the Asiatic part of the country, the range occupies the whole of the Middle Asian plains. The southern border either goes beyond the borders of our country, or passes along the foot or foothills of the southern moun-791 tain systems. Thus, the range does not include Tarbagatai and Dzhungarsk Alatau, but passes between them, as well as along the Il'i valley and Il'iisk depression to China. Farther west, the southern border skirts the Tien-Shan system; apparently, the Fergana Valley together with Karatau are included in the range, and it skirts around the Pamiro-Alaisk montane country. It crosses Zeravshan valley near Pendzhikent and passes around the Baisunsk mountains or occupies their southern foothills and Kugitangtau.

To the east, the marbled polecat is encountered in the Surkhandar'ya valley, at least up to Denau and Saryassiya, in the Babatag (between Surkhandar'ya and Kafirnigan), along the lower Kafirnigan (apparently, not reaching Dushanbe); along the Vakhsh, it penetrates as high as Kurgun-Tyube, and along the Pyandzh it apparently reaches the mouth of the Kyzylsu, and perhaps to Kulyab. Apparently, the animal is more widely distributed in southern

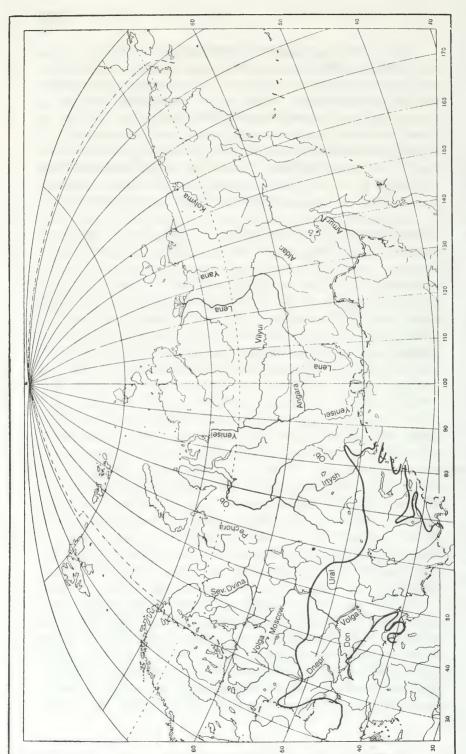


Fig. 280. Reconstructed range of marbled polecat, V. peregusna Güld. in USSR V.G. Heptner.

Tadzhikistan along river vallies and low dry mountains than has been shown. Besides being an undoubted inhabitant of the plains, however, the marbled polecat penetrates along valleys high into the mountains in some places (Tien Shan) and is even recorded at heights up to 3000–32000 m.

To the west of the Amu-Dar'ya, the range of the marbled polecat exits beyond state borders everywhere. It is, however, absent in the Kopet-Dag, although in the lower western parts of the range, it penetrates into the mountains, notably along the foothills and valleys.

The assumption about the inhabitation of the marbled polecat in the Trans-Urals to 54° 50′ N. lat. (Kundrava southeast of Chelyabinsk—not 55° 30′ as written by Ognev, 1935) is a mistake and is, apparently, based on an imported skin. The affirmation of its existence around Baikal, whence a separate form was even described, and in "Siberia" (Pocock, 1936) is not well-founded—this species is absent everywhere east of the Cis-Altai steppes in our country.

In the last 100–200 years, the range of the marbled polecat has been contracting significantly. This decrease started from the west. Thus, information about the occurrence of the marbled polecat in Belovezha reflects the boundary in the 18th and 19th centuries; in Volyn' and Podolia" it existed in the first half of the last century; in Moldavia ("Bessarabia") it disappeared about 100 years ago. Near Odessa, the animal existed even at the end of the first half of the last century, but by the 70's, it had already disappeared and later appeared occasionaly and very rarely (Fig. 281).

In the west, beyond the Dnepr, this animal is now absent and almost everywhere it has even been completely forgotton. At the beginning of our century (before 1914), the marbled polecat was only recorded twice on the right bank of the Dnepr—near Kiev and near Odessa. These were, obviously, transgressions, although it cannot be excluded that near Odessa, it could have appeared from Romania. From there (from Dobrudzh) transgressions to Izmail'sk district are not excluded even now.

The border has shifted very strongly eastward, even east from the Dnepr. Occurrences near Pavlograd and around Zaporozh'e have to do with the beginning of our century (to 1914). In vast expanses, though not everywhere, between the Dnepr and the Ural, the northern border of the range has also shifted to the south.

Thus, at the beginning of the current century in Orlovsk district, the marbled polecat still existed, although it was rare, but in 1925, it had already completely disappeared. At that time or somewhat later, the marbled polecat also disappeared from Kursk district.

In the 50's of the present century the western boundary of the marbled polecat's range was represented a line of complicated outline (details insufficiently known), going at first from Voronezh (Voronezh preserve) southwest to Kupvansk or to a place between them and Khar'kov, and thence to Krasnograd-already the right bank of the Donets. Here the border swings sharply southeast and passes through Artemovsk to Lyugansk. Somewhere on the right bank of the lower Donets, the border swings back sharply to the southwest and goes straight west some distance from the shore of the Sea of Azov to Osipenko city or a little westward—to the meridian of Melitopol.³

In the interfluve between the Dnepr and Volga, the northern 792 border, begins near Voronezh, descends somewhat southward, and then, passing slightly north of 50° N. lat. directs itself eastward to Khoper. Thence, it crosses over the Volga at an unknown point, to the middle course of the Uzenei on the interfluve of the Volga and Ural [river] (Saratov district).

Individual occurrences of the marbled polecat were registered, already long ago, both west and north outside the outlined area of present distribution—these are Poltava (perhaps even a more or less permanent occurrence), and Pugachev in Trans-Volzh'e.

On the whole, the border of the range for the last 100-200 years receded very strongly—from north to south (not to mention the right bank of the Dnepr) for 350-600 km, and from west to east for 700-1000 km. The latest shift of the range led to that this "rounded pontoon" ring which the primordial range formed in its western part was shown to be broken, and the union between populations of extreme southeastern Europe (Romania, Bulgaria) and the southeastern part of our country (Don and Volga steppes) was already absent. Reduction of the range in the south and east in the European part of the country continues and apparently, the complete disappearance of the marbled polecat, at least in the expanse between Dnepr and Don, is not far off. At present, the

³Sokur (1960) demonstrated its occurrence also in Nikolaevsk district (Vladimirsk region); however, this place was not shown in the map and no details are reported.

1193

marbled polecat is already only sporadically distributed, rare or even very rare everywhere west of the Don; in many regions it appears occasionally and is obviously on its way to complete disappearance.

The reason for the marbled polecat's disappearance lies in the ploughing of the virgin steppes with which it is associated, and in the complete agricultural utilization of the steppe and forest-steppe, and in particular, in the disappearance of ground squirrels. The area of their normal and more or less continuous distribution begins east of the Don (at Kamensk, Shakt and others), and in the Cis-Caucasus.⁴

It is very interesting that reduction of the range of the marbled polecat in Europe proceeds in parallel the expansion of the steppe polecat's range. Replacement of a species associated with the virgin steppes—"a fugitive of culture"—by another carnivore of its lineage ecologically analogous in many ways, but revealing a tendency towards being a "companion of culture". They secure for themselves subsequent prosperity where the marbled polecat does not persist. No competitive relationships between these species was observed in sufficiently extensive areas of sympatry.

In the east, reduction of the range remains almost unobserved. Changes recorded there belong, apparently, to the category of negligible natural fluctuations in the border of the range.

Fossil remains of the marbled polecat have been found only within the limits of its recent range.

Geographic Range outside the Soviet Union

In Europe the range includes Dobrudzh in Romania (in remaining part of Romania, only transient in Krainovo district near Danube), all of Bulgaria, eastern and southern parts of Yugoslavia (Serbia, Kosovo and Mefodia, northern Macedonia, southern Adriatic coast; in Slovenia, transient in extreme northwest of country, European

⁴Range according to data of Brinken, 1829; Kessler, 1850; Eversmann, 1850; Greve, 1894; Miller, 1912; Dinnik, 1914; Satunin, 1915; Brauner, 1923, Averin, 1928; Migulin, 1929, 1938; Calinesscu, 1930, 1931; Nezabitovskii, 1934; Ognev, 1935; Flerov, 1935; Pocock, 1936; Ptushenko, 1936; Charleman', 1937; Vereshchagin, 1947, 1959; Kuznetsov, 1948, 1952; Stroganov, 1948, 1962; Korneev, 1952; Sludskii, 1953; Dal', 1954; Heptner, 1956; Barabash-Nikiforov, 1957; Chernyshev, 1958; Afanas'ev, 1960; Sokur, 1960; Ishunin, 1961 and other sources and unpublished material of N.I. Larina and V.G. Heptner.

794

part of Turkey and easternmost part of Greece, west approximately to Salonika (Calinescu, 1930, 1931; Brink, 1958; Markov, 1959; Dulic and Tortric, 1960).

In Asia, the range occupies the Mongolian Republic north to 47° (southern foothills of Khangai, Undurkhan) and to 49° (west-793 ern great lakes region), Inner Mongolia, including Ordos⁵, Afghanistan, Baluchistan, Iran, Iraq, Syria, Palestine and Asia Minor (the details of its distribution here are unknown)*. Probably, the range goes on to Kashgaria, but positive information about this is absent (V.H.).

Geographic Variation

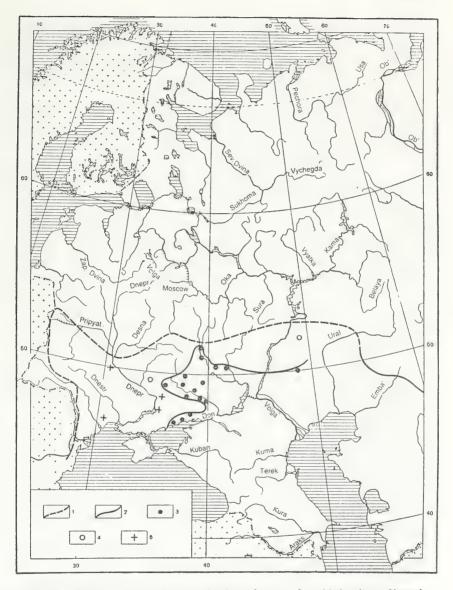
Geographic variation of the marbled polecat is still poorly studied. In all, about 12 geographical races are known, of which more than half belong to our territory. This number is, apparently, exaggerated, for there are not more than three real subspecies in our country. The fundamental characteristics of all forms are based on coloration. At the same time, as shown above coloration of the marbled polecat is subjected to very strong individual variation. In several cases, general dimensions or claw length were given as characters, and craniology not given at all.

Great variation of color, commonly based on limited material, was presented by several authors, especially older ones (for example, K.A. Satunin) but also recent, is clearly in error. All these are responsible for contradictions, both in interpretation of various forms, and also in descriptions of their color characters as well as distribution. Thus, in the opinion of one author (Stroganov, 1948), in the nominal form the white band on the forehead is broken, while all other authors describe it as continuous; in another case, the distribution of the form *negans* was found to be disjunct, and between the two parts of it lies the range of another form (Novikov, 1956), etc.

Based on considerable material (Z[oological] M[useum of] M[oscow] U[niversity]), a preliminary scheme is given below of the geographic races recorded in our country, and in part, in

⁵Shanxi but not Shaanxi as some authors write, i.e. inside the great northern bend of the Huang He and not on the left bank of the river west of it.

^{*}But see Harrison and Bates, 1991. The Mammals of Arabia, 2nd ed. Harrison Zoological Museum.



793 Fig. 281. Some previous and present borders of range of marbled polecat, Vormela peregusna Güld, in the European part of USSR. V.G. Heptner:

1—Reconstructed northern and western borders of range (western more or less approximate);
 2—The recent (at beginning of 60's) northern and western borders;
 3—Separate points of occurrence in last decade;
 4—Separate distant transgressions in last decade (Poltava, Pugachev);
 5—Some peripheral places of occurrence in beginning of 20th century (before 1914). Map depicts formation of the break in "rounded pontoon" ring of original range.

adjacent ones. It was ascertained that the main feature of geographic variation of color lies not in detailed color difference, but first of all, in its general tone, mainly on the dorsal body, and in the ratio of darker to lighter colors (density of spots, their general area) in the saddle-patch.

Since statements of some authors (Stroganov, 1962) on differences in size between races have not been confirmed, dimensions of the separate forms are not given.

1. South Russian marbled polecat, V. p. peregusna Güeldenstaedt, 1770 (syn. sarmatica, intermedia, euxina).

General color dark. Basic prevailing color of dorsal saddle dark rusty-brown or brown and sometimes dark- or blackish-brown. Light spots on it relatively small and few, bright brownish-yellow, yellow-straw or whitish-yellow color. Three longitudinal occipital stripes, and lateral separated from dorsal and not fused anteriorly (no "collar" formed). Color of occipital stripes pale-yellowish, sometimes white. Scapular stripes well marked, thigh stripes often distinct; however, they always bear dark spots. The white frontal band not divided medially, and does not unite with peristomal white ring or very rarely forms one. Abdominal spots absent, or in all 1–4 may occur and they are small and dull.

In the south and southeastern European part of the country, Cis-Caucasian steppes and probably the Trans-Caucasus. Boundaries with respect to the next form unknown.

Outside the USSR-in Romania and the Balkans.

The systematic position of the marbled polecat of the Trans-Caucasus has not been studied in the manner required. They have been related (Ognev, 1935) to the population inhabiting the eastern Cis-Caucasus ("intermedia") on the basis of very little material. It is possible that they belong to syriaca—a form which in general is very little known.

2. Transcaspian marbled polecat, V. p. koshevnikovi Satunin, 1910 (syn. alpherakyi, tedschenica, obscura).

General color dark. Basic prevailing color of dorsal saddle 795 dark-brown or even blackish-brown—similarly dark or darker than the nominal form and with less red tinge. Light spots few, for the most part light-yellow or white in color. Occipital stripes united anteriorly by a broad transverse white stripe (forming well-defined "collar"). Color of lateral occipital stripes usually yellowish. Scapular stripes very distinct; of thigh, weakly defined and bearing dark

spots. White frontal band not divided medially and has no connection with peristomal ring. Abdominal spots are absent or rarely occur, weakly defined and few (1-3). Claws short—the longest less than 10 mm.

In the western part of Middle Asia—eastwards to at least Amu-Dar'ya and region of right tributaries of Pyandzh and upper Amu-Dar'ya (southern Tadzhikistan). Distribution eastward beyond Amu-Dar'ya and boundary with next form not clear—apparently, however, does not pass to east of Karatau [range] (see below). Border with nominal race also unclear.

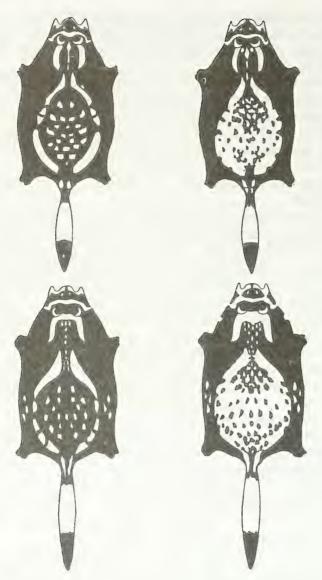
Outside the USSR—Iran, Afghanistan, West Pakistan (Baluchistan).

The Transcaspian marbled polecat represents a well-defined race, close to the nominal form. It is very similar to the latter in dorsal color, but dark tone often even darker and therefore fur color appears more contrasting. Except for this indistinct character, both forms are well differentiated from each other by the presence of a "collar" in the Transcaspian form.

The dark form described from southern Tadzhikistan (*obscura*) has in general a completely similar type and intensity of color. Characteristics of head coloration mentioned by the authors of the original description are not constant, and do not have essential diagnostic significance. The author's suggestion concerning its small dimensions not confirmed (Chernyshev, 1956). Although the author considers this form "one of the most differentiated subspecies" (Stroganov, 1948), there is insufficient basis to separate it from the Transcaspian *V. p. koshevnikovi*. Moreover, its range (valleys of Vakhsh and Pyandzh) is perhaps very small. Such small ranges are not characteristic of races of Palearctic carnivores.

The forms peregusna and koshevnikovi as a pair of closely related dark forms, contrast sharply with the very light pallidior and, apparently, to its pair member—negans.

The presence of dark races which shows no essential characters of "degradation" of color in Turkmenia and southern Tadzhikistan and, apparently, in Afghanistan—countries with clearly defined desert climate and in general, desert conditions—is, in some respects paradoxical. In a series obtained from Turkmenia, one may find skins having purer, more saturated black tones, generally with more contrast (brightness) than among the nominal race. It is notable that such races occur even in the middle part of



795 Fig. 282. Schematic drawings of color of several forms of marbled polecat, (from Ognev, 1936, with modifications). Upper row—extreme types of color variation of South Russian marbled polecat V. p. peregusna Güld (on right specimen from Cis-Caucasus); lower row—Transcaspian marbled polecat V. p. koshevnikovi Sat. (on left) and Semirech'e marbled polecat, V. p. pallidior Strog. ("negans"). There are substantial differences in the form of the lateral occipital and finely dotted stripes as well as general development of black and light colors on dorsal saddle.



796 Fig. 283. Marbled polecat surveys its surroundings before coming out of its burrow, Kyzyl-Dzhar village in Badkhyz preserve, southern Turkmeniya. May 1962. Photo graph by A.A. Sludskii.

the Kara-kum (Uch-Adzhi; Z[oological] M[useum of] M[oscow] U[niversity]). The very light color of the Semirech'e and Central Asiatic animals clearly contrast with this form. There are, therefore, two groups of race of marbled polecat—the dark European, Near Asiatic (Afghanistan, Iran) and western Turkestanian races, and the light—Semirech'e (eastern Middle Asiatic) and Central Asiatic races. Such a division of race groups reveals certain analogous features known in some other carnivores (weasels, badgers, bears).

The name adopted here for the Transcaspian form has an indisputable priority over *alpherakyi** Birula, under which this form is usually known, although both of them appeared in the same year.

3. Semirech'e marbled polecat, *V. p. pallidior* Stroganov, 1948 (the name *negans* was applied to this form).

General color light. Prevailing color of dorsal saddle light, changing from ocherous-yellow to almost white, often straw yellow. Over it, are scattered sparse tawny, brown or rusty-brown

797

^{*}In Russian original misspelled alhperakyi—Sci. Ed.

spots. Occipital spots in its anterior part connected by a transverse white stripe ("collar" well developed). Color of lateral occipital stripes whitish. Scapular stripes not sharply defined, but due to generally light color of dorsal saddle, are well marked. Thigh stripes undefined or almost undefined and strongly covered with spots. The white frontal band often divided by narrow (up to 1 cm) medial black stripe, but has no connection with white peristomal white. Light spots are encountered fairly often on abdomen and are usually larger. Claws quite long—reaching 13 mm. on middle digits of fore foot.

In the region to east of the Karatau range, Semirech'e, Cis-Altai steppes and montane steppes of southern Altai (Chuisk).

Outside the USSR—in Dzhungariya, and Mongolian Republic, apparently except in southeastern or eastern parts.

A well-distinguished form, obviously contrasting with both previously described forms. It is possibly the lightest form of the species, or in any case of members of the group of light races (see above). Based on its color type, it represents a sort of negative of the races of the dark group—the ratio of dark to light areas on the dorsal body and saddle are reversed.

Despite the obviousness of characters of the Semirech'e population in the sense of comparison to several other races and distributions—this, of the many forms, is the least known and unclear. The Semirech'e marbled polecat was previously (Ognev, 1935) considered as transitional from the Transcaspian V. p. koshevnikovi ("alpherakyi") to the Central Asiatic (Ordos) V. p. negans or was allocated directly to this race. In any event, its differences from the Transcaspian form were emphasized, which is completely correct.

A clearer delimitation between the forms pallidior and negans than that followed (Stroganov, 1948) is required. On the other hand, the limits of the distribution of this form to the west are unknown. The suggestion that it is distributed "from the eastern slopes of Karatau...southward, apparently, to Turkestan and the Alaisk (in the text, in error as Altaisk; V.H.) range" (Stroganov, 1948, 1962), is not understandable. In general, the race inhabiting the area between the Amu-Dar'ya in the west, Karatau in the east, and Turkestan and the southwestern spurs of the Gissar range in the south is not clarified. In any case, considering the Semirech'e pallidior, there is no basis for relating animals from Uzbekistan and Tadzhikistan to the form negans as is sometimes done (Novikov,

1956). This view was, apparently based on misunderstanding since such a gap in the range of a race is improbable.

Note. Pocock (1936) described a separate form of marbled polecat V. p. ornata from "the vicinity of Lake Baikal". Judging by the photograph, this form is of moderately dark color with a well developed "collar"; i.e., an eastern type. However, as is known, the marbled polecat is absent not only in the vicinity of Baikal (if one may speak of proximity to a lake extending for about 1000 km from north to south), but also in a great area around it. The author had 2 more specimens from "Siberia", and he proposes "Siberia" as the region of distribution of this race. To establish that it particularly represents the form ornata is not in any way possible and this name is best excluded in the category of nomen delendum.

* * *

Beyond the borders of the USSR, the following forms are indicated (not counting *euxina*, see above, and *ornata*): *V. p. negans* Miller, 1910—Ordos, Inner Mongolia, Shaanxi and some other parts of Inner Asia, not accurately clarified, and possibly also eastern or southeastern parts of the Mongolian Republic; *V. p. syriaca* Pocock, 1936—Syria and adjacent territories (Palestine?) eastward to western Iraq.

Note. V. p. chinensis Stroganov, 1962 described from a specimen labeled "China" and earlier assigned to negans (Ognev, 1935) does not deserve separate status. The nature of area inhabited (and origin of the type) is set forth as "basin of the lower course of Hwang Ho". None of the arguments in use leads to such an interpretation of the label, not to mention that in the lower course of Hwang Ho if that part of the river below the great northern bend can be so considered, the marbled polecat is entirely, apparently, absent. At the same time, it was shown (Bannikov, 1954) that, judging by the route of the collector (Pyasetskii), this marbled polecat was caught at the southern border of the Mongolian Republic, i.e. in the region inhabited by the form negans and not

far from its type locality (V.H.).

Biology

Population. Almost everywhere the marbled polecat is encountered in the European part of the country—they are few in number; it is, with few exceptions, a rare animal. In the Don and Kuban steppes, it was comparatively common in the 20's. In the Cis-Caucasian steppes, the marbled polecat was most common in the eastern part of the steppes (Kizlyarsk steppe) where it is drier. There it is most often met with at the present time (V.G. Heptner). The marbled polecat is now common in Kazakhstan, in the Muyunkum sands, southern Pribalkhash'e, and along the Syr-Dar'va (Sludskii, 1953). The marbled polecat is most common in Turkmenia, where its distribution is closely connected with the great gerbil [Rhombomys opimus] and it is encountered formerly in great numbers, in the flat part of the country it was the most common small carnivore. Its population significantly exceeds the weasel population (V.G. Heptner).

Habitat. The marbled polecat is an animal of open unwooded expanses—dry steppes, semideserts and deserts. It is met with chiefly in places rich in large desert and steppe rodents—gerbils, ground squirrels and in part jerboas, etc. The ploughing of virgin steppes and fallow lands pushes out the marbled polecat and reduces its range. It is encountered in the southern grass steppes of the chernozem zone, does not avoid thickets of blackthorn, buckthorn and other shrubs in steppe shelterbelts. It infrequently occupies afforested river valleys and the borders of forest massifs of 799 the forest-steppe. It is encountered occasionally among gardens, melon fields or even in settlements; but in dry hilly steppes, it is rare. In Middle Asia, it mainly inhabits localities of desert and semidesert character, but it does not avoid river valleys and sections cut by irrigation ditches and sometimes overgrown with a border of tamarisk. It is most common in stabilized slightly hilly sands, sprinkled with black saxaul, winterfat, pea-shrubs [Caragana] and milk-vetches [Astragallus] alternating with solanchak with scattered saxaul woods. In sagebrush-grass semideserts, serozem sagebrush deserts, clayey steppes and sheep's fescue-feathergrass foothill steppes, it is met with rarely (Sludskii, 1953). The marbled polecat prefers the plains and for the most part does not go higher than the foothills. It inhabits woodless mountains covered with



798 Fig. 284. Marbled polecat running in grass. Badkhyz preserve, southern Turkmenia.

May 1962. Photograph by Yu.K. Gorelov.

montane steppes. In Talysh, it is rarely found more than 2000 m above sea level and in Tien Shan—up to 3000 m.

Food. Information on foods of the marbled polecat is scarce. Apparently, of greatest significance in Middle Asia are the various species of gerbils, especially the great gerbil with which it is always closely associated, and the long-clawed ground squirrel [Spermophilopsis leptodactylus]. The marbled polecat feeds on other ground squirrels [Spermophilus], jerboas, hamsters and various mouse-like rodents. In captivity it eats small animals, birds, lizards and eggs. Cases of attacks on domestic fowl are unknown.

Home range. Information is absent.

Burrows and shelters. The marbled polecat for the most part inhabits burrows of various steppe rodents, only widening and deepening them. In Turkmenia, and generally in Middle Asia, the marbled polecat lives permanently in colonies (towns) of great gerbils, not only because of the close trophic connection with this rodent but also in connection with its use of the complicated underground structure as a diurnal shelter in case of danger and during reproduction. It sometimes uses burrows of long-clawed



799 Fig. 285. Marbled polecat in colony of great gerbil, *Rhombomys opimus*. Badkhyz preserve, southern Turkmenia. May 1962. Photograph by A.A. Sludskii.

ground squirrels, but this is an exception. The marbled polecat does not make its own burrows as a rule (V.G. Heptner).

Daily activity and behavior. The marbled polecat is mainly active in twilight and early morning. It spends the day in burrows (Sludskii, 1953). In Turkmenia in winter time, spring and autumn, when the heat is still not too great, daytime activity occurs in the marbled polecat or morning hunt is sustained longer—when sun is very high. As a kind of exception, the animal appears on the surface during the day in summer time (V.G. Heptner).

The marbled polecat hunts for great gerbils under the ground. The predator, penetrating the subterranean passages of a town, causes great disturbance among its inhabitants—the gerbils run out from the burrows, hided again in them, try to run across to neighboring colonies, etc. The hunting marbled polecat appears first in one burrow and then another, disappears underground again, and again appears, etc. In open expanses, following, for instance, widely wandering midday gerbils [Meriones meridianus], the marbled polecat rarely catches them; mainly it catches them in burrows (V.G. Heptner).



800 Fig. 286. Tracks of marbled polecat on wet sand in a gallop and scheme of leaps. Foot prints are placed in fours—hind feet do not fall in the tracks of fore feet. Karakum 80 km to north of Ashkhabad, 25 January, 1948. Sketch by A.N. Formozov, about 2/3 of natural size.

A characteristic behavior of the marbled polecat manifests itself in the intimidation pose which it displays in case of fear. In a defensive pose, the tail is raised especially strongly up over its back (like a squirrel). At the same time, it rises up high on its legs, jerks up its head and bares its teeth. In contrast to the "chirring" of polecats, ermine and weasels, it gives a peculiar growl like a dog. The frightening effect is strengthened by the bright, variegated black-and-white fur. When running, the marbled polecat expands its tail, fluffing it out.

Seasonal migrations and transgressions. Data are lacking.

Reproduction. In the northern Caucasus, estrus occurs in March (Rossikov, 1887; Satunin, 1915). In Pribalkhash'e (Kazakhstan), a pregnant female was noted in the first days of February (Sludskii, 1953). Throughout March, females which already had given birth

801

to young were caught. In the northern Caucasus, parturition occurs later. On 9 May, there was a litter of six still completely helpless young (Rossikov, 1887). In Kazakhstan, parturition occurs, apparently, in February-beginning of March (Sludskii, 1953). The 8-week period of pregnancy occurring in the literature probably does not agree with actuality. The number of young in a litter ranges from 3 to 8. The average number (from 13 cases) is 4.3. Thus, the marbled polecat is less fecund than the steppe polecat.

Males, it seems, participate in raising the young. Spermatogenesis begins to be extinguished in April.

Growth, development and molt. Information is absent.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. This carnivore has no dangerous enemies. The steppe polecat may be named as one of the most fundamental competitors influencing the distribution and numbers of the marbled polecat. Other steppe carnivores hardly exhibit a noticeable influence as competitors.

The marbled polecat is almost unsusceptible to plague, and more susceptible to tularemia.

Human changes in the virgin steppes and their ploughing lead to the displacement of the marbled polecat and to a sharp decrease in their numbers. Utilization is not large and has no effect at all on the number of the marbled polecat (P.Yu.).

Practical Significance

The importance of the marbled polecat as a fur-bearing animal is negligible. In the USSR, slightly more than one thousand skins are taken annually. Its fundamental significance is as a predator which destroys steppe rodents, vectors of dangerous infections. Its role in destroying rodents harmful to agriculture is not great since the marbled polecat is rare in agricultural regions, and it avoids cultivated landscapes. On the whole, it is a useful animal (P.Yu.).

Genus of Honeybadger or Ratel*

Genus Mellivora Storr, 1780

1780. *Mellivora*. Storr. Prodr. Meth. Mamm., p. 34. tab. A. *Viverra ratel* Sparrmann = *Viverra capensis* Schreber¹.

Dimensions large.

Limbs plantigrade, forelimbs with very long, strong claws, of fossorial type. Webbed membrane between digits absent.

Skull massive and broad, with voluminous elongated braincase. Facial portion short and broad, the palate wide, paroccipital and mastoid processes large, strongly projecting (mastoid width is approximately equal to zygomatic). Auditory bullae large and swollen. Auditory tube covered from above by anterior part of mastoid process and opens below it. In general appearance, the skull is entirely similar to skulls of representatives of the subfamily of true martens.

Dentition of cutting (sectorial) type, with strongly developed carnassial teeth (above, fourth upper premolars; below, first molars); upper first molar relatively very small and strongly elongated in transverse direction. On the whole, dental system is quite similar in its main features (structure and relative size of teeth, etc.) to that of species of the subfamily of true martens, Mustelinae, especially polecats. The essential difference is only in that the second lower molar is, as a rule, absent.

Dental formula
$$I \frac{3}{3} C \frac{1}{1} P \frac{3}{3} M \frac{1}{1} = 32. **$$

Ear pinna reduced and represented by short dermal ridge. Subcaudal glandular "pocket" absent, anal orifice located in a deep pouch radially striated by thickened skin; anal glands large and gives off secretion with a sharp odor.

Pelage coarse and sparse, coloration of dorsal saddle type. Teats, 2 pairs.

*The Russian common names medoed and lysie barsuk are literally "honey-eater" and "bald badger" respectively—Sci. Ed.

¹The generic synonyms, since they are not used in the Russian literature, are not given.

**In Russian original, erroneously given as $I = \frac{3}{3} C = \frac{1}{2} P = \frac{3}{3} M = \frac{1}{1} = 32$ —Sci. Ed.

An omnivorous predator, mainly feeding on small vertebrate and invertebrate animals. Ecologically, it is an entirely flexible form, encountered chiefly in different types of flatlands, mainly open, to sandy deserts inclusively, but it avoids continuous moist tropical forests; it is met with mountains. Its capacity to dig is well developed.

The range of the genus is vast and includes the major part of Africa and Near Asia, India and the western parts of Middle Asia (for more details, see below, species description).



Fig. 287. Range of genus of honeybadgers, Mellivora Storr. and species range of ratel or honeybadger, Mellivora capensis Schreb. Schematic. V.G. Heptner.

Within the boundary of the genus, many species were described, especially at the end of the last century and beginning of the current one, both from Africa and also from Asia. At the present time, it was established (Pocock, 1941) that the genus includes only one species, with several races. This viewpoint may be considered generally accepted.

The independence of the genus *Mellivora* has never been considered in doubt. However, the attempts made to establish its systematic position and phylogenetic relationships with other groups within the family led, and for the most part still lead, to quite large discrepancies. In the 60's of the previous century, the honeybadger was assigned to the badger group, and this view is held, in part, to the present day. Those who do not assign it directly to the badgers—subfamily Melinae—in all events, closely affiliate 803 *Mellivora* with Melinae. At the same time, the similarity between honeybadger and badgers is actually purely external, and expressed in general measurement, color type and, as is clearly assumed, general appearance of the animal (see beyond).

It is likely that the viewpoint is still more widely accepted, according to which the genus *Mellivora* forms a separate subfamily Mellivorinae close to the subfamily of badgers, Melinae, a "neighbor" so to speak, to it.

At the same time, as was in part mentioned above (see also beyond), according to skull, both in main features and many details of dentition, the genus reveals greatest similarity to species of the subfamily of martens, true Mustelinae, and is strongly differentiated from the badger group, Melinae. The latter have different dentition both in structure and adaptive type, that is particularly expressed in structure of the posterior upper molar and in other characteristics (see beyond). According to the sum of all features, the genus *Mellivora* cannot and must not be united with the badger subfamily, Melinae, and it is very difficult to argue for its separation into an independent subfamily. Genus *Mellivora* must be considered as one of the typical, but specialized, forms of the marten subfamily, Mustelinae. This view of the position of this genus within the subfamilies was also previously expressed.

Within the boundaries of the subfamily Mustelinae, the genus *Mellivora* is, to a certain extent, analogous to the genus of wolverines, *Gulo*. If the wolverine is actually a specialized deviant gigantic marten, the honeybadger may be considered a huge

aberrant polecat, including also in this designation the above-mentioned (p.1179) African genera of polecats².

An opinion was expressed about some genetic connection of honeybadger with wolverine, but it is without serious foundation.

Because of the closeness of the genus *Mellivora* to the remaining Mustelinae, the significant distance of the genus from *Meles* and the subfamily Melinae in general points to the systematic position of the skunk (*Vonyuchka**) group, subfamily Mephitinae. They are clearly considered to occupy an intermediate position between "Mellivorinae" (honeybadger) and Melinae (badgers). However, it is indubitable that, according to dentition for instance, skunks are sharply differentiated from the honeybadger and all Mustelinae, and are much more similar to badgers (Melinae). Therefore, the gap between g[enus] *Mellivora* and members of the subfamily of badgers, Melinae, is very sharp and deep. Nowadays, the subfamily of skunks is restricted in its distribution to the New World only, but in the past (upper Miocene–upper Pliocene) it was also found in the Old—in Europe and in Asia.

With all of this, the uniqueness of the genus *Mellivora* remains without doubt. Its independence is also shown by its relatively long period of existence—from the middle Pliocene (Asia). The genus *Eomellivora*, nearest to *Mellivora*, is known from the upper Miocene and existed as several species during the course of the whole Pliocene both in the Old world (Eastern Europe—Odessa district and Moldavia; Asia), and also in America. The early relationships and origins of both genera are unknown, but *Eomellivora* is evaluated not only as a quite typical form close to *Mellivora* but also as a more specialized genus than *Mellivora* in some respects. In general, the origin of the group is associated with the primitive Mustelinae (Thenius and Hofer, 1960).

In the genus there is one species: *Mellivora capensis* Schreber, 1776.

The forms of the genus are, apparently, practically indistinguishable.

In the USSR, distributed in the western part of Middle Asia, and associated with deserts and desert mountains.

It has no practical significance (V.H.).

²According to their dentition which may consist of 28, 30 and 36 teeth in different forms, they are even more strongly differentiated from the true Mustelinae than the honeybadger.

^{*}A Russian word literally meaning "stinking" animal or person—Sci. Ed.

RATEL OR HONEYBADGER3

Mellivora capensis Schreber, 1776

- 1776. Viverra capensis Schreber. Säugeth. pl. 125. Also: 1777, 3, pp. 450, 588. Cape of Good Hope.
- 1792. Ursus indicus. Kerr. Animal Kingdom, p. 188. India.
- 1851. *Mellivora ratel*. Horsfield. Cat. Mam. E. Ind. Co., p. 120. India.
- 1920. *Mellivora wilsoni*. Cheesman. Journ. Bombay Nat. Hist. Soc., 27, p. 335. Ram-Khormuz on the Iran-Iraq boundary.

Diagnosis

Only species of the genus.

Description

In general proportions, appearance, and behavior, the honeybadger is entirely unique and, in spite of the prevalent opinion, does not resemble the badger. It more quickly reminds one of a bear-cub on the one hand, and on the other, it has much in common with the polecat. It often moves in a sort of creep, extending its body, bending its back and raising its tail upright.

Trunk quite heavy and massive, moderately elongated, tail short, limbs short but quite thick and strong. Head quite large and broad compared to body dimension, with blunt facial portion. Bare nose tip large, anteriorly flattened, black in color. Ear pinna greatly reduced and represented by short dermal ridges. Limbs with relatively large, broad feet, the lower surface of which is bare in winter and summer. Fore paws typically fossorial. Their claws very long, laterally compressed and moderately bent. Their distal halves are light-horn, basal—dark-horn. Length of longest claw 32–46 mm. Claws of hind limbs relatively large, but much shorter than those of fore limbs; their length 10–18 mm. They are darker, more massive and strongly bent, quite wide and almost completely covered by hairs of upper foot.

³ "Medoed" [Honey-eater] is an artificial name, representing a translation of the Latin generic name. Another name exists, among, Russian hunters in southern Turkmenia and it has the sense, "to use". This species is called by Turkomen "it-aii"), which means "dog-bear" (it—dog).

Description given mainly from material in ZMMU.



804 Fig. 288. Ratel, or honeybadger, Mellivora capensis Schreb. Sketch by A.N. Komarov.



805 Fig. 289. Ratel, or honeybadger, *Mellivora capensis* Schreb. Kushka—Kashan interfluve, southern Turkmenia, 1960. Photograph by Yu.K. Gorelov.

Winter fur is long (hair length on posterior part of back 40-50 mm), closely-lying and consisting of coarse elastic, even somewhat bristle-like hairs. They are quite sparse (parting the hairs anywhere, one sees the skin), and without underfur, or it is very weakly developed. On sides, hairs noticeably sparser than on back; on belly, particularly on groin and axillae hairs extremely rare and here skin shows through strongly. Hairs on tail approximately of same length as on posterior part of back.

Summer fur sparser and shorter—hairs on back have length of about 15 mm. On belly, fur still sparser—it is half bare.

Skin very thick. Anal glands well developed. Teats, 2 pairs.

In winter fur, entire lower body-belly, throat, chin, lower surface of tail and its terminal hairs, and also lateral surface of body-side of head including ears, side of neck, outer surface of limbs as far as the middle of shoulder blade and middle of thigh as well as anterior part of muzzle including eye region—is a shiny black color. Sometimes, the fur has a very light brownish tinge.

On top of head, a little behind the eyes, a white area begins, having an arched anterior border and covering the whole upper body. This runs over the upper neck as a narrow band, in width corresponding with the area on the head, sometimes even a little narrower, gradually broadening in the shoulder region and reaching its greatest width in the middle of the trunk or nearer the thighs. At the tail base, this area strongly narrows and extends as a narrow band occupying the whole upper side. The hairs on the very end of the tail are black. On the whole, it has a typical dorsal saddle pattern extending, however, to the neck, head and the upper side of the tail. In a stretched skin, the light area has a pear-shaped or flask-shaped form with a narrow "extension" on the tail.

The general tone of this area is white, but in details of color, the dorsal saddle is somewhat variable. Hairs on the head and 806 upper neck are usually white to their base. Sometimes, however, their bases are somewhat darkened and they are slightly visible against the general white background. Hairs white to the base, or with weakly developed darkening at the roots form a narrow band edging the dorsal saddle from shoulder to thighs. The remaining main part of the saddle patch is covered by hairs with a white distal half and with a wide dark base. These bases more or less (usually strongly) shine through, and the whole area has a unique color a mixture of pure white and dark tones resembling the color

of gray with remains of black hairs ("salt and pepper"). The white tone is cold and only sometimes has a light ocherous film. The above-mentioned edge band of pure white hairs is sometimes, especially with a strong admixture of dark in the saddle patch, is separated in the form of a fuzzy lightening on the general background, and sometimes the edge of the saddle patch also has the same color as in the middle part.

The summer fur has the same color as in winter, but the color of the light dorsal field is more intensively mottled with dark, with the pure white areas on the neck and head absent—they are of the same color as the middle of saddle patch. Sometimes in its posterior part, a lighter narrow border is noticed. In different individuals, the dark tone is visible through the white, sometimes more and sometimes less, and the general color is lighter or darker but these differences are, apparently, small.

Sexual differences in color are absent, and age differences are undescribed. Among the exotypic variations, malanism is known (Africa). The geographic variation in color, if present, is very weak.

Skull relatively large and quite heavy, of entirely unique structure⁴. The upper profile of the skull presents itself as a quite even, arched line having its highest point in the parietal; quite quickly descending posteriorly, and very gently sloping forwards without any rise in the interorbital region. The profile of the nasal opening, which is greatly displaced backward, serves as a continuation of this line with a small projection. The facial part of the skull, although wide, is short; its length is approximately two times shorter than the braincase.

The postorbital constriction is long and very narrow—its width is always less than that of the interorbital area, usually considerably so (by 5–10 mm). The braincase is large—elongated and wide, broadening posteriorly and swollen in the parietal region. The occipital crest is strongly developed, and the sagittal is relatively weak (much weaker than in the badger) even in the very old animals. Zygomatic arches are strong but not very massive, in the medial portion arching upwards very strongly. The lateral lines of the interorbital region are parallel or almost parallel, the supraorbital processes have wide bases, but are short.

⁴The skull of the honeybadger is often compared to the skull of the badger as the most similar. This was based on misunderstanding. One may see similarity only in general dimensions and known massiveness; generally the skull of the honeybadger is more quickly recognized as the skull of an enormous marbled polecat.

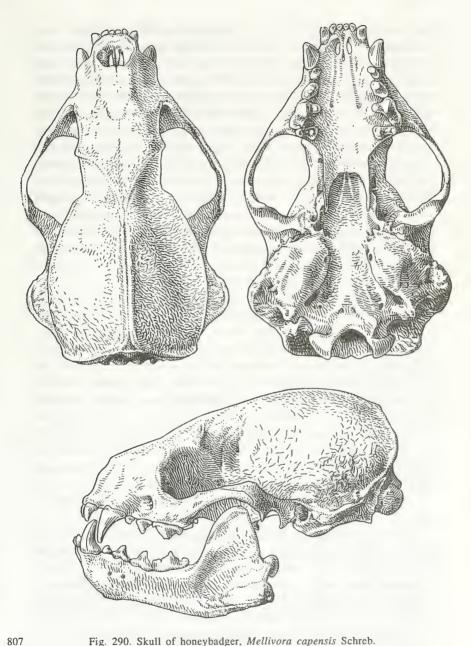


Fig. 290. Skull of honeybadger, Mellivora capensis Schreb.

The mastoid processes are developed very strongly, situated almost horizontally, and strongly projecting to the sides, whence the mastoid width of the skull is greater than the zygomatic, or at least equal to it. Mastoid processes are flattened, and dorsally even somewhat concave. Their lower surface fuses with the upper wall of the auditory tube⁵ and the posterior part passes to the occipital crest. The paroccipital (lateral occipital) processes are large, separated both from the occipito-articulars and also from the auditory bullae and greatly projecting ventrally and somewhat externally.

Bony auditory bullae very large, swollen, angular-oval and strongly diverging anteriorly—their anterior walls adhere closely and partially fuse with inner parts (those directed towards sagittal plane of skull) of postarticular processes. Hard palate short and wide; its interior width between molars 2.5 times less (or about that) than distance from posterior median sphenopalatine notch to alveoli of middle incisors. Portion of palate lying behind toothrow relatively short and broad. Infraorbital foramen small, its diameter not more than half diameter of upper canine alveolus.

Dentition strong and massive with short apices, wide at base. Carnassial teeth particularly massive, having large main cusp with wide base and well-developed, quite wide secondary inner blade. Upper molar quite typical of martens and polecats—small, strongly elongated in transverse direction and its transverse diameter almost double longitudinal (anteroposterior). Inner blade considerably greater than outer; they are separated by a marked isthmus. Canines strong and massive, broad at the base, but quite short. Anterior upper premolar relatively large, having two roots. In contrast to that observed in previously described species of subfamily Mustelinae, and also in badgers and, in part, in otters, there is no tendency towards reduction or loss of this tooth.

Sexual differences in skull structure are absent or not noticeable, and no age variation has been described.

The os penis has, in terminal quarter, a sharp bend upwards—tip located nearly at right angle to axis of proximal half. Tip itself not evenly divided—one "horn" is larger than the other (Pocock, 1941). In general, structure is typical for martens and polecats (subfamily Mustelinae) and differs strongly from that characteristic of badgers.

The body length of males (2) is 680-750 mm, of females (1), 680 mm; tail length of males is 180-205 mm, of females, 172 mm; length of hind leg in males is 120-125 mm.

⁵It is indicated (Pocock, 1941) that "the cavity of the long swollen auditory capsule posteriorly opens into the hollow of the mastoid process".

Condylobasal length of male skull (3) is 139.5–145.7 mm, of females (1), 130 mm; zygomatic width of males (3) is 80.0–86.2 mm, of females (2), 75.2–80.3 mm; mastoid width of males (4) is 82.8–86.4 mm, of females, 80.7 mm; interorbital width of males (4) is 31.7–33.8 mm, of females (2), 32.0–32.6 mm; postorbital width of males (4) is 23.6–27.5 mm, of females (2), 27.7–30.5 mm; width of muzzle above canines in males (4) is 32.5–34.6 mm, of females, 30.8 mm; length of upper toothrow (without incisors) in males (4) is 38.5–40.2 mm, of females (2), 30.8–37.2 mm.

Weight of male is 12 kg (September) and 16 kg (October), of female, $9.1~{\rm kg.}^6$

There is sexual dimorphism in body and skull measurements—the females are smaller than the males—but they are relatively insignificant. Difference in overall weight is more obvious (V.H.).

Systematic Position

Only species in the genus.

Geographic Distribution

Africa, a large part of Near Asia, India, western Middle Asia. The range of the ratel is one of the most extensive of the species ranges in the family.

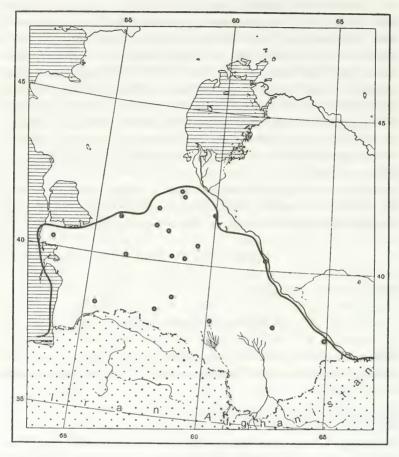
809 Geographic Range in the Soviet Union

The range is not great, and constitutes a very small part of the species range—its extreme northern part, and occupies an insignificant part of the country.

The southern border of the range within the boundaries of USSR coincides with the state frontier from the Caspian Sea to Amu-Dar'ya. Occurrence and places of permanent occupation of

⁶From material of Z[oological] M[useum of] M[oscow] U[niversity] from Turkmenia, collected by A.M. Shukurov, I.V. Zhernovov, V. Svyatoi, S.I. Bil'kevich, E.I. Shcherbina, A.N. Sukhinin and from one specimen collected by Varentsov (Ognev, 1931).

Measurements of Indian animals (Pocock, 1943) are: body length of males (5) is 690–725 mm, of females (2), 625–650 mm. Condylobasal length of male skull (6) is 131–141 mm, of females (6), 121–132 mm; zygomatic width of males (8) is 74–80 mm, of females, (5), 71–76 mm. Weight of male (2) (time [of year] is not mentioned) 9.7–10.4 kg, of females, 7.7 kg. Data relate to both Indian subspecies. The maximum body length of Indian animals of 82.5 cm (Novikov, 1956) is apparently a misprint.



809 Fig. 291. Limits of distribution of honeybadger, *Mellivora capensis* Schreb. in the USSR. Dots indicate several separate habitats in Karakum and other deserts of Turkmenia. Many known occurrences of the animal along boundary of range between Amu-Dar'ya and Caspian Sea not plotted. Data of 1962. V.G. Heptner.

the ratel are known along the Atrek [river], along the entire Kopet-Dag [range] and nearby Kopet-Dag plains, along the Tedzhen and the Gyaz'-Gyadyk mountains (right bank of upper Tedzhen), throughout the whole Badkhyz (expanse between the Tedzhen and Kushka) and in the highland area between the Kushka and the upper Murgab. Apparently, the honeybadger also exists in the area from the Murgab to Amu-Dar'ya—it was found on the left bank of the upper course of this river in Khalach region.

The western border on the north is formed by the Caspian coast, to a little north of Krasnovodsk. Thence or slightly further north (south shore of Kara-Bogaz-Gol), the northern border of the range begins. It passes to Kazakhla village in the southern Ustyurt Chink (in the place where the borders of Turkmenia, Kazakhstan and Karakalpakia meet) and Kaplankyr and farther along the Chink 810 (Aganash, Kurgankyr, Zangibaba), occupies Sarykamyshsk depression, and through Deukal village (Deukaskenkala, Onkhauz and Doudyr), generally at the latitude of Kunya-Urgench, and somewhat to the west of it reaches the Amu-Dar'va delta. In the delta itself and in its contiguous cultivated lands, in particular the Khiva oasis, the honeybadger is not, apparently, encountered. From the Kunya-Urgench district, the border turns to the southeast, becoming the eastern border of the range and, apparently passing around Khiva oasis, and going farther along the Amu-Dar'ya, reaches the state border. In the middle course of the river, the ratel was recorded at Darganat (tugai) and in the upper course, it was recorded, as noted above, at Kalach near Kerka.

The honeybadger has not been recorded on the right bank of Amu-Dar'ya and is, apparently, absent there. The Amu-Dar'ya constitutes an insurmountable barrier for this species dispersing from the south—from Iran and Afghanistan.

Inside the outlined region, the ratel has been noted in a series of places, not only in clay deserts along the chinks of the desert plateau, in declivities in mountains, river valleys "pistachio savanna" etc. but also in sandy deserts, both with saxaul and without. Apparently, the distribution of this species within the borders of our country is more or less continuous, although its numbers evidently predominate to the south, and in areas with a more or less interrupted relief and with more compact soils. Within the boundaries of the described region, the ratel is known, for example, from the following places: Sharlouk in the south of western Turkmenia, a little north of the Atrek river and west of Karakal; sand 60 km north of the railway station Geok-Tepe; Bala-Ishem well in the Usboi 150 km north of Kyzyl-Arvat railway station; Bakhardok well between Ashkhabad and Sernyi zavod [factory]; sands of Tedzhen region; Iolbarsli well (north of 38° N. lat. and a little east of the 60° E long.); railway station Uch-Adzhi between Mary [Mery] on the Murgab and Amu-Dar'ya (sands); Darvaza

(northwest of Sernyi *zavod*) Kyrkkaya (100 km east of Darvaz), Zaunguzsk Karakum, and others⁷:

Beyond that, in the beginning of the 90s of the previous century, when the first information on the occurrence of honeybadgers within the borders of our country appeared (Bikhner and Zarudnyi, 1892: Varentsov, 1894) there was no information at all about it for a long time, and the prevalent opinion was that it appeared occasionally among us, or in any event, represented an extreme rarity. New data appeared only in 1918 (Bil'kevich, 1918) and in the 20's (Ognev and Heptner, 1929). From these, it was clear that the honeybadger, although rare, lived permanently in the Kopet-Dag. and across the directly adjacent plains in extreme southwestern Turkmenia—from the Tedzhen to the Atrek. It was later elucidated that it occurred at furriers in these places starting from 1924, although in small numbers (individual animals). Suppositions concerning the great rarity and extremely limited range of the ratel with us persisted until recent times (Novikov, 1956—"very rare", "exclusively southern Turkmenia").

Investigations in the 50's and the very beginning of the 60's and, to a lesser extent, in the 40's, showed that the ratel is not at all rare in the country, being distributed northward to the Ust'yurt and occupies the whole Karakum. It was shown to be not rare even at the extreme northern border of its range in the USSR, and is quite common in the south. Apparently, one may think that at present the honeybadger occurs more often in Turkmenia than the badger [Meles] and is more widely distributed. It is significant that in Turkmenia, at least in the southwestern half of the country, the honeybadger has a special popular name. Russian hunters also have a special designation for it (see above).

Undoubtedly, the present picture of the range and population of the described species, appearing completely unexpectedly, the result of wide zoological investigations which have unfolded in Turkmenia in the last ten years. However, there was also an increase in numbers of the species at least in the south, where it undoubtedly became much more abundant than in the first quarter

⁷The honeybadger is found in a great number of places along the above-mentioned southern frontier of our part of the range. They are not listed.

Range according to Bil'kevich, 1918; Ognev and Heptner, 1929; Sukhinin and Shcherbina, 1955; and unpublished material of V.G. Heptner, and mainly Yu.F. Sapozhenkov, Yu.K. Gorelov, I.V. Zhernovov, I.V. Svyatyi, V.P. Kostin, and collections of Z[oological] M[useum of] M[oscow] U[niversity].

of our century, and the borders of its range shifted to the north. Nothing be said about the extent of its increase in numbers and the period during which it took place. In any event, the present northernmost habitats lie at a distance ranging from 350 km (at the 56° E. long.) to 650 km (along longitude 59° E. long.) from the previously known ones (10's and 20's) and the more eastern parts even farther—up to 800–850 km. Settlement proceeded both from the direction of Afghanistan and from the direction of Iran, but was probably more intensive in western Turkmenia and thence into its northern and northeastern parts. Despite being a large eurytopic species, sandy deserts are for it, seemingly less favorable.

Geographic Range outside the Soviet Union

In Africa, the honeybadger is distributed at present from the extreme south (Cape region) northwards to Ethiopia, northern Somali and Sudan (Suakin near Port Sudan on the Red Sea). In the past, it is evident that it also occupied the regions adjacent to the Nile in Egypt and reached the Mediterranean Sea in this part of Africa. However, the northern border of the range in Africa is quite indefinite. Judging by features of the species described from the Trans-Caspian part of the range, in the east, it apparently passes generally keeping to the 20° N. lat. along the southern edge and in the southern parts of the Sahara, and in the west, it is, apparently, more northerly—along the hills of the Ennedi desert, Tibesti, Adrar-Iforos and others. In any event, its presence was established on the Air plateau (Asben, 1800 m above see level). Thence, the border of the range passes in an unclear way through the western parts of the Sahara to southern Morocco (Ifni, Sus and the Valley of Umer-Ryabii, a little south of Casablanca). In the Sahara, the ratel only avoided probably, its northeastern parts, notably the Libyan desert. The range probably does not include the inner parts of the forested region of West Africa, although it has been recorded in the Congo (Ituri region).

In Asia, the range includes Syria, Palestine and the Arabian Peninsula, Iraq (except, probably, the northern parts), the greater part of Iran⁸, Afghanistan (except, probably, the higher parts of the

⁸Missone (1959) refers to the range of ratel in Iran as very limited and clearly incomplete, believing that it may, however, exist in other places. According to this author, honeybadger inhabits only a small territory in the extreme southwestern corner of the country (in Khuzistan) between the head of the Persian Gulf and the southern contd. on next page

Hindu Kush), India, from the former Northwest Frontier Provinces to Bengal inclusive (absent in Assam and Burma), northward to the foot of the Himalayas and the southern zone of Nepal, in the south to the sea coast—to the southern extremity of the peninsula. It is, apparently, absent in the Malabar coast. In Ceylon, it is absent. In the described reconstructed range it has apparently not undergone essential changes, except in Egypt (V.H.).

Geographic Variation

With so significant a range, the ratel undoubtedly displays known geographic variation; however, it is not, apparently, great. Thus, the differences between the two "polar" forms—the South African capensis and the Indian indica—lie in insignificant differences in color and in the somewhat smaller average dimensions of the Indian subspecies. The two Indian subspecies differ insignificantly from each other only in density of the fur (Pocock, 1941).

About 15 subspecies in all have been described, almost all from a single specimen. There is no special revision of geographic variation in the species.

Within the boundaries of the USSR, there is only one form, apparently, not differing in any substantive way from the Indian.

Indian honeybadger, M. c. indica Kers, 1792.

For characteristics of this form, see above.

Western part of Middle Asia northward to the southern Chink of Ustyurt, and eastwards to the Amu-Dar'ya.

Outside the USSR—in Afghanistan, Iran (except, perhaps, the southwestern), [West] Pakistan and the western part of India (not east of southern Nepal).

Two forms are usually considered to exist in the territory of Hindustan—indica and inaurita. They differ from each other only in that in the second (eastern) the fur is somewhat denser, and hairs are found on the heel. It is assumed that this form may also be found in the provinces contiguous to Afghanistan (Pocock, 1941)

contd. from previous page

half of the border with Iraq. On the other hand, its range was described as a narrow belt along our borders from Tedzhen to the Gorgan (Astrabad) Gulf on the Caspian Sea. Judging by the distribution of the species in the USSR and in neighboring countries and by its biological characteristics, one may allow that it exists over the whole of Iran, except probably the northwestern, maybe, the wooded region of the Elbrus mountains (it was, however, found near Gorgan city; Bil'kevich, 1918) and the vast deserts of the middle and eastern parts of the country (Dash't-e-Kavir, Dash't-e-Lut). Proceeding from these data, the range is given in the map (Fig. 287).

although this is not quite understandable (Pocock's text is contradictory). Since our honeybadgers live under more severe conditions (winter) than those under which the Indian form lives, it is possible that the fur of the former is denser than that of true *indica*, *i.e.* it is like *inaurita*. However, the differences themselves between these forms are doubtful: our museums have no materials of these races and therefore the name given is retained for our animals. The relationship to the form *wilsoni* from southwestern Iran is perhaps unclear, but judging from everything, this form, described from individual characteristics of one specimen, does not have substantial truth.

* * *

The following forms are usually described from parts of the range lying outside the USSR. Independence of a series of these forms, including Palearctic ones, is doubtful. 1) *M. c. inaurita* Hodgson, 1836—Nepal and parts of the range east of it⁹; 2) *M.c. wilsoni* Cheesman, 1920—southwestern Iran, Iraq (?); 3) *M. c. pumilio* Pocock, 1946—Hadramawt, southern Arabia; 4) *M. c. leuconota* Sclater, 1867—West Africa northwards to southern Morocco; 5) *M. c. signata* Pocock, 1909—Sierra Leone; 6) *M. c. consica* Thomas et Wroughton 1907—Lake Chad; 7) *M. c. buchanani* Thomas, 1925—Air plateau (Asben), Sahara; 8) *M. c. abyssinica* Hollister, 1910—Ethiopia; 9) *M.c. broekmani* Wroughton, 1920—Somalia; 10) *M. c. cottoni* Lydekker, 1906—Ituri region, Congo; 11) *M. c. makwelli* Thomas, 1923—Kenya; 12) *M. c. sagulata* Hollister, 1910—Tanganyika; 13) *M. c. vernayi* Roberts, 1932 Bechuanaland; 14) *M. c. capensis* Schreber, 1776—South and Southwest Africa.

The actual number of forms of honeybadgers is, evidently, smaller. This is clear at least from comparison of the places whence several forms were described (abyssinica-broekmani; leuconota-signata; consica-buchanani; indica-wilsoni) (V.H.).

Biology

Population. Everywhere within the boundaries of the range in the USSR, it is not often encountered, but it is not particularly rare. Numerical indices of population do not exist.

⁹The suggestion of "Northwestern Frontier Provinces", *i.e.* contiguous to Afghanistan (Ellerman and Morrison-Scott, 1951) is hardly correct. It contradicts the main data of Pocock's monograph (1941) and other indications of these same authors (distribution of the form *indica*).

Habitat. Within the limits of natural landscapes in its range, the honeybadger may be called a eurycious species. It is met with in sands of the Karakum; in sands and foothill plains of the Kopet-Dag range; in montane canyons of the latter; among steppes and hills of Badkhyz; in marsh tit* plains covered with saxual, Russian thistle [Salsola] and sagebrush; among deep ravines of the southern precipice of Ust'yurt [plateau] with stunted vegetation of shrubs, sagebrush, and succulent saltwort; in cultivated river valleys among the bai** landscape; and in dense riparian tugai thickets.

Food. Insufficiently studied. In India, it feeds on small rodents, birds, reptiles including cobra, as well as grasshoppers, miner bees, wasps and their larvae and honey. In India, they sometimes attack poultry-yards. Its bias towards honey is noted in South Africa.



Fig. 292. Habitat of honeybadger at northernmost range border. Precipices—biotope of arkhar [O. ammon]. Foot of southern Chink, Ust'yurt, Kazakhly village.

Photograph by V.P. Kostin.

*The Russian word (pukhlyakoba) means marsh tit, but its significance as a descriptor of landscape is unclear—Sci. Ed.

**bai is a Turkïc word referring to a wealthy landholder in Middle Asia; i.e., river-valley land—Sci. Ed.

According to data collected in the most recent period in the USSR, the honeybadger may be called an omnivorous animal. It eats plant food in captivity; in nature, this event is unknown. In its food, remains of great gerbils occur repeatedly, and it also eats hedgehogs; a case of eating the carcass of a lamb was observed (Kostin, Sapozhenkov, Gorelov, Zhernovoi and Svyatoi, 1963). Among reptiles, feeding on the desert monitor was recorded in Badkhyz (Sukhinin and Shcherbina, 1955 and others). It very often feeds on Horsfield's tortise which it digs out even in winter. Small lizards and round-head lizards [Phrynoce-phalus] also occur in its food. At the southern edge of Ust'yurt (V.P. Kostin), up to 30% reticulate scales of Phrynocephalus were found in feces. Among insects, grasshoppers were found, in particular the saxual humpbacked grasshoppers, and darkling beetle (Sapozhenkov, Kostin, Zhernovoi and Svyatoi, 1963).

Home range. Information is lacking. On the edge of the Ust'yurt, tracks of honeybadger were traced for a distance not less than 2.5 km; it follows that, the home range is quite large (V.P. Kostin).

Burrows and shelters. The honeybadger lives in burrows dug by itself. It digs very well, and is able to dig a tunnel into very hard ground in 10 minutes. The honeybadger usually digs simple burrows with one passage and nesting chamber. The dimensions of the latter: 37 × 43 and up to 60 cm. Bedding does not occur in the nesting chamber. The length of the burrow is not large: from 1 to 3 m. The diameter ranges from 17–18 to 30 cm, more often 25–30 cm. The distribution of burrow depth ranges from 25 cm 814 to 1.5 m. Apparently also occurs in rocky shelters. In Ust'yurt, an accumulation of feces—a "latrine"—was found in a small cave among limestone blocks (V.P. Kostin).

Daily activity and behavior. The honeybadger has no regular rhythm of daily activity. As a rule, it leads a crepuscular-nocturnal way of life (Sapozhenkov et al.; 1963; V.P. Kostin), but is sometimes active during the day, especially in March-April, on warm, sunny days. Its daily activity has been observed in India. In South Africa, it is usually active during the day.

Seasonal migrations and transgressions. Information is absent. Reproduction. Until recent times, nothing was known about reproduction, except that in South Africa, a female gave birth to two cubs after a 6-month pregnancy.

Signs of rut were noticed in female in Ashkhabad Zoo at the end of September. A male caught on 10 October, had large testes. In Ashkhabad Zoo, a female caught on 6 May delivered on



814 Fig. 293. Habitat of honeybadger in the northern limit of its distribution in northern Karakum. Arkhar also live here and rarely cheetah and leopard. Kaplan Kyr village, southern Chink, Ust'yurt. Autumn 1962. Photograph by Yu.F. Sapozhenkov.



814 Fig. 294. Hilly landscape in Badkhyz preserve, southern Turkmenia. Habitat of ratel or honeybadger. May, 1961. Photograph by Yu.K. Gorelov.

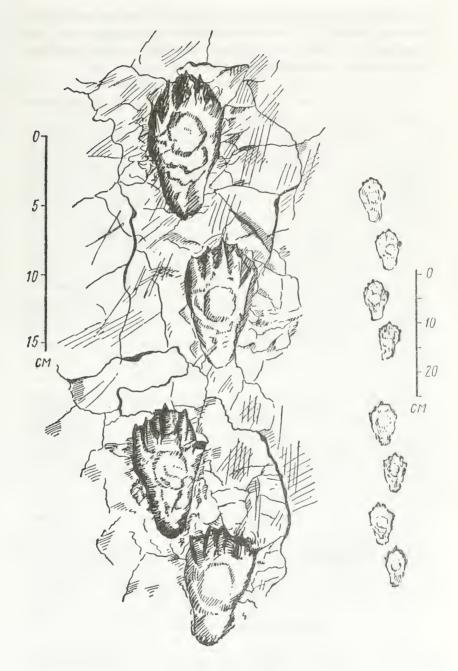


Fig. 295. Tracks of honeybadger. Sketch by V.P. Kostin.

31 May; she gave birth to one cub. In the first days of May, a lactating female and cubs with erupted teeth and opened eyes was observed. The duration of pregnancy, therefore, is about 7 months, which is close to the South African data.

Growth, development, and molt. Information is lacking.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. Data are absent.

Field characteristics. The color of the honeybadger masks it very well in solonchaks. Moving in an uneven gallop, it is very reminiscent of the general form of the wolverine. Prints of its tracks are wider and shorter than the badger. Its feces have a sausage-like form, 4–7 cm long and 12 mm diameter. Becoming angry, it raises its tail upward when walking (V.P. Kostin).

In addition to the gallop, by which the honeybadger can proceed for a prolonged time, it also walks and even half-crawls, sprawling on the ground. The voice of the honeybadger resembles a hoarse "khrya-ya-ya-ya". At the time of rut, the male makes a loud grunting sound (Sapozhenkov et al., 1963). The honeybadger climbs trees well. It gives off a frightening smell and exceptional movement of the skin surface (P.Yu.).

Practical Significance

Due to its small numbers and because it inhabits little-populated places, it has almost no practical significance. It is not hunted especially and is for the most part captured accidentally. Honeybadger are sometimes caught alive for zoos. For this, the animal's tracks are followed and they are dug out from burrows (Sapozhenkov et al., 1963). (P.Yu.).

Subfamily of Badgers

Subfamilia MELINAE Burmeister, 1850

Genus of Badgers

Genus Meles Brisson, 1762

1762. Meles. Brisson. Regn. Anim., p. 13. Ursus meles Linnaeus, 1758.

1795. Taxus. Cuvier et Geoffroy. Mag. Encyclop., 2, p. 187. Ursus meles Linnaeus, 1758.

1925. *Meledes*. Kastschenko. Zap. Fiz.-mat. vidd. Ukr. akad. nauk, I, No. 4. *Meles leptorhynchus* Milne-Edw. Described as a subgenus. (V.H.).

Dimensions large.

General conformation heavy and clumsy; body relatively short, considerably wider posteriorly than anteriorly; head relatively small; tail short. Limbs not shortened, massively plantigrade with long claws of digging type; webbing between digits absent. Ear pinnae normally developed. Hair cover coarse, long but sparse, with weakly developed underfur. Coloration from combination of black and white, type of saddle-patch developed to an extreme degree. Between the anal opening and root of tail there is a glandular "pocket", into which an odorous secretion exudes. Anal glands well-developed. Teats 3 pairs—2 abdominal, 1 inguinal.

Skull quite massive and heavy, but not broad, moderately high. Braincase not of increased volume, facial part of skull elongated and narrow (its length more than its width), that part of hard palate lying behind toothrow long and relatively narrow, mastoid processes well developed but not very large, paroccipital processes well-defined, but short. Mastoid width of the skull is considerably less than zygomatic. Auditory bullae of moderate size and not swollen. Auditory tube not covered by mastoid process and opens independently in front of it.

Dentition is a specific type, fundamentally differing from that characteristic of Mustelinae. It represents a combination of teeth of a sectorial type with those having clearly defined structural features of a tuberculo-grinding (crushing) tooth. The structure of the dentition is one of the most characteristic features of the subfamily. It is more similar to the dentition of the subfamily of otter (Lutrinae). Upper carnassial tooth not largest in toothrow—it is short and triangular in form. Upper molar is largest, considerably larger than carnassial, flat, tuberculate and of grinding type. Lower carnassial tooth elongated. All cheek teeth, except upper molar, are of more or less distinctly sectorial type.

Complete dental formula is $I\frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{1}{2}=38$. However, individual first premolars or all of them are frequently lost and

the formula changes correspondingly (see below, description of species).

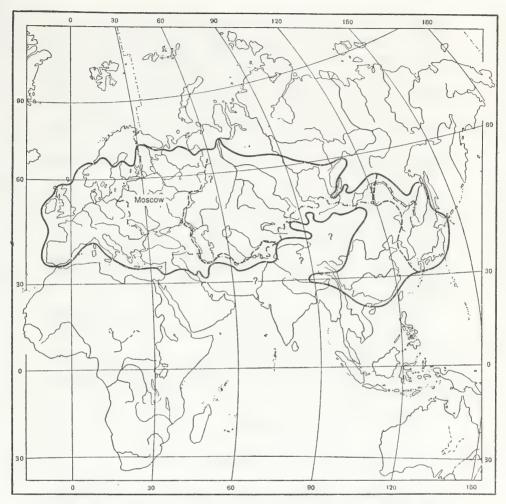
They are omnivorous forms, feeding mainly on invertebrates and small vertebrates. Ecologically they are entirely flexible and are encountered from closed taiga and broad-leafed forests to steppes and semideserts, and in part true deserts; they do not avoid mountains and are met with at great heights. Digging capability is strongly developed. There is a latent stage in development of fertilized eggs, and winter sleep.

The range of the genus is vast and occupies Europe, a considerable part of Siberia, Near, Central and Eastern Asia as well as Middle Asia.

In the current century, several species were included in the genus other than the European M. meles—Cretan M. arcalus, Asiatic M. leptorhynchus, Tibetan M. leucurus and Japanese M. anakuma. For our fauna, two species—M. meles and M. leptorhynchus—were accepted. In actuality, separate species must not be distinguished in the genus. Even the extreme races, as regards their distribution and their characters, as well as their form are interrelated. The differences between them, as between M. m. meles and M. m. amurensis, may be very great in color and even dentition (in the European badger, there are as a rule 38 teeth and in amurensis—34).

The circle of genera in the subfamily includes besides Meles, the genera Taxidea (American badger), Arctonyx (Indian "sand" badger), Helictis (including Melogale:* "ferret" badgers of southeastern Asia) and Mydaus (teledu—Malay archipelago). All of them are sharply distinguished from each other (Helictis is sometimes separated in an independent subfamily) and it is difficult to establish their systematic relationship. The genus Meles may be, apparently, considered in this sense a little specialized form, although its dentition is in some respects (development and relationship between upper molar and carnassial) more specialized than in some other forms. Apparently, Meles stands closest to the American Taxidea, to which it is most similar in general appearance. Taxidea must, however, be considered on the whole and particularly in its skull, a more specialized form, although it is somewhat inferior to Meles as regards specialization of the dentition. The southern Asiatic Arctonyx, also closely related to Meles, is usually considered a

^{*}This is now the accepted name for the genus of ferret badgers—Sci. Ed.



818 Fig. 296. Range of the genus of badgers, *Meles* Briss., and species range of the common badger, *Meles meles* L. Borders of the range in Afghanistan, China and, in part, in the Indochinese Peninsula are to a certain extent given approximately. Dotted lines separate the regions of the distribution of the main race groups of badgers—European *meles*, Siberian—Chinese "sandy" badgers, *arenarius-leptorhynchus*, and Far East badger, *amurensis-anakama*. A question mark in the region of the watershed of Kama and Pechora points to the unclear limit between the two race groups.

V.G. Heptner.

more specialized form (Pocock, 1941), although, apparently, without sufficient basis.

Very primitive representatives of the subfamily, or forms close to it (*Broiliana*, *Stromeriella*) are known from the early Miocene of Europe and Asia. A series of genera which indicate the great

variety of forms of the group are known from the upper Pliocene of the Old World. The majority of them, however, as regards the line leading to the genus *Meles*, represent lateral branches with various specialization (*Palaeomeles*, *Plesiomeles*, *Taxodon* and others). Aside from them, *Parameles* (Odessa), *Melodon* and *Parataxidea* stand closest of all to the genera *Meles* and *Taxidea*.

818 Parataxidea is known from the upper Miocene and lower Pliocene of Asia and is widely distributed, itself representing a separate, more specialized, group. Melodon must be considered the source of the genus Meles.

The genus *Meles* itself appeared in the upper Pliocene from whence are known *M. gennevauxi*, *M. taxipater*, and *M. thordi* and from which through *M. m. atavus* the line leads to modern *M. meles*. This is, apparently, the typical Asiatic form, developing without close connection to the American badger (*Taxidea*) which is known only from America (upper Pliocene). It is, apparently, related to the Asiatic *Parataxidea*.

The genus includes one species: *Meles meles* Linnaeus, 1758. In practice, the forms of badger are of little positive importance (fur, destruction of some pests).

In the USSR it is distributed throughout the greater part of the European territory of the country, through the southern half of Siberia and the Far East, and in Middle Asia (V.H.).

BADGER

Meles meles Linnaeus, 1758

- 1758. Ursus meles. Linnaeus, Syst. Nat. Ed. X, 1, p. 48. Uppsala, Sweden.
- 1785. Meles taxus. Boddaert. Elench. Animal, 1, p. 80. Europe.
- 1816. *Meles europaeus*. Demarest. Nouv. Dict. Hist. Nat. Substitute for *meles*.
- 1844. *Meles anakuma*. Temminck. Fauna Japonica, Mamm. p. 30, pl. 6. Vic. Nagasaki, Japan.
- 1847. Taxidea leucurus. Hodgson. J. Asiat. Soc. Bengal, 16, p. 763, pl. 29. Lhasa, Tibet.
- 1859. *Meles taxus amurensis*. Schrenck. Reisen und Forsch. im Amur-Lande, p. 17, pl. 1, Fig. 1. Amur near mouth of Ussuri [rivers].

- 1867. *Meles leptorhynchus*. Milne-Edwards. Ann. Sc. Nat. Zool., 8, p. 374. Vic. Peking [Beijing], China.
- 1875. Meles canescens. Blanford. Ann. Mag. Nat. Hist., 16, p. 310. Abadekh, between Shiraz and Isfahan, Iran.
- 1891. *Meles schrenkii*. Nehring. Sitzungsber. Ges. Naturf. Freunde Berlin, p. 103. Substitute for *amurensis* Schrenck.
- 1895. *Meles taxus arenarius*. Satunin. Arch. Naturg., 1, p. lll. Rynpeski, between lower Volga and Ural [rivers].
- 1899. *Meles meles typicus*. Barrett-Hamilton. Ann. Mag. Nat. Hist., 4, p. 384. Substitute for *meles* Linnaeus.
- 1900. Meles taxus sibiricus. Kastschenko. Kashchenko. Opredelitel' Mlekop. Zhiv. Tomskogo kraya, plate 15. Former Tomsk governance. Restricted to (Stroganov, 1962) Kolyvan', about 400 km north of Novosibirsk.
- 1901. Meles amurensis altaicus. Kastschenko. Kashchenko. Ezhegodn. Zool. muzeya I. Ak. nauk, 6, p. 613. Southern end of Teletsk Lake, Altai.
- 1901. *Meles amurensis raddei*. Kastschenko. Kashchenko. Ibidem., p. 613. Steppes of Trans-Baikaliya.
- 1905. *Meles meles minor*. Satunin. "Priroda i okhota", No. 2. Borzhom, Trans-Caucasus.
- 1907. *Meles blanfordi*. Matschie. Wiss. Ergebn. Filchner Exp. nach China, 10, 1, p. 143. Kashgariya.
- 1910. *Meles tianschanensis*. Hoyningen-Huene. Zur Biol. d. estländ. Dachases, p. 63. Tyan'-Shan' [Tien Shan].
- 1913. Meles melanogenys. J. Allen. Bull. Amer. Mus. Nat. Hist., 32. p. 433. Musan on Tumangan river, northern part of Korean Peninsula.
- 1916. *Meles meles ponticus*. Blackler. Ann. Mag. Nat. Hist., 18, p. 75. Skalita near Trabzon (Trapezund), [Trebizon], Asia Minor.
- 1926. *Meles meles caucasicus*. Ognev. Uchen. zap. Sev-Kasvk. inst. kraevedeniya, 1, p. 50. Vic. Vladikavkaz.
- 1926. *Meles meles tauricus*. Ognev. Ibidem. 1, p. 51. Beshuisk forestry camp in Chatyr-Dag, Crimea (Crimean preserve).
- 1931. Meles leptorhynchus talassicus. Ognev. Zveri Vost. Evropy i Sev. Azii, 2, p. 478. Southern slope of Talassk Alatau, western Tyan'-Shan' [Tien Shan].
- 1931. *Meles meles heptneri*. Ognev. Ibidem., p. 775. Aleksandro-Nevskaya north-west of Kizlyar, eastern Cis-Caucasus.
- 1940. *Meles meles severzovi*. Heptner. Zeitschr. f. Säugetierk., 15, p. 224. Arkit, south of Syry-Chilek Lake, south of the north-

eastern extremity of the Chatkal range, Tyan'-Shan' [Tien Shan].

1962. Meles meles aberrans. Stroganov. Zveri Sibiri, 2, p. 167. Akmolinskaya district, Bogembai village, northern Kazakhstan (V.H.).

820

Diagnosis

The only species of the genus.

Description

General body constitution heavy and massive, especially in full winter pelage. Entire body seems to possess a wedge-shaped form—the broad and convex posterior half suddenly narrows anteriorly and, through the short ill-defined neck, passes to the relatively small, narrow, obviously elongated head. From the ear region, the head, continuing the general outline of the body, the wedge proceeds to the noticeably elongated, narrow facial portion with the somewhat extended, quite movable nose.

Limbs short and massive, plantigrade with naked lower surface of feet. Claws strong, elongated (on middle digit of fore limb, 30–35 mm along curve, 22–26 mm in straight line) and obtuse at end, adapted to digging. Tail short, approximately equal to head length. Ear pinna relatively very small, rounded. Bare tip of nose quite large, separated from mouth margin by narrow band of fur. Eyes are small.

The animal usually moves slowly and heavily, as if listless, lowering its head. The posterior part of its trunk appears higher than the shoulder and the general appearance is depressed. The badger does not flex the back as martens, polecats and wolverine do, and does not stand erect like the honeybadger. However, it can run quickly at a gallop.

In winter fur, pelage on back and sides is long and coarse, consisting of coarse, even bristly guard hairs and sparse quite soft undercoat. The venter is covered with short, sparse hairs and skin is usually visible in the inguinal region. Length of guard hairs on the middle of the back in winter is 75–80 mm.

821

Color of the Middle Russian badger in its winter fur coat, *i.e.* late in autumn before retiring for the winter is as follows. Throat, lower neck, chest and legs black, venter black with light brownish



Fig. 297. Badger, Meles meles L. Sketch by A.N. Komarov.

820

tints, inguinal regions brownish-gray. General color tone of dorsum and sides is a beautiful and pure light silvery-gray, as if coated with translucent black ripples. On the sides, there are straw-colored highlights, more in the lower part. Such coloration is determined by differently colored guard hairs which have a broad (35–38 mm) dirty-whitish or straw-whitish basal part, and after it a wide (22–25 mm) deep black band and a white or slightly grayish-white tip 10–12 mm long. On the sides, bases of hairs have more intensive straw tone, the black band is somewhat narrower, and

ends of the hairs is white¹. The tail is covered by long coarse hairs, quite fluffy, and generally of the same color as the back.

The head is white, with white covering lower lips and chin also, where it is sharply bordered by the black throat. Two pure black bands pass along the head, sharply differentiated from the white background. Each of these begins on the upper lip at the mouth opening anterior to the corner of the mouth, and initially passes directly upwards. Somewhat below the level of the eye, the bands pass backwards at a right angle and, rising somewhat upwards and getting wider, pass through the eyes and, getting still wider, cover the whole base of the ear and even a part of the parietal region. In this region, its width is greatest.

Behind the ear, the band, sometimes widening somewhat again, extends along the dorsolateral part of the neck sometimes to its middle (sometimes noticed somewhat farther back) and here disappears, gradually merging with the color of the upper body. Sometimes, it slants downwards between the color of the side of the neck (corresponds with back color) and the white field below. The width of the band anteriorly is about 15 mm, and in the ear region it is 45–55 mm. The black tone of the band is more intense in front of the eye, between eye and ear, around the ear and directly behind it. In the anterior section, the band frequently has a dirty or grayish tone and its outline is not sharp. Most frequently, the initial vertical portion of the band is weakly defined or almost undefined.

The black facial bands outline a wide white band with almost parallel sides which extends from the nose tip through the [midline of the] forehead and crown. This band covers the occiput and the anterior part of the neck and sometimes almost the whole neck, gradually merging with the color of the upper body. Sometimes it does not lose its breadth and sometimes it tapers to a point and is quite well outlined.

The white fields of the ventro-lateral surface of the head extend backwards as a wide band of quite even width, between the black color of the lower head and neck and the black head band. Posteriorly, these [lateral] bands usually extend to the same distance as the upper [mid-dorsal] white band, and sometimes more—they occur notably on the greater part of the neck's length between

¹Sometimes it is stated that along the badger's spine, gradually spreading out posteriorly, runs a brown band. This is a misundertstanding—such a pattern is absent in our badgers.

the gray color above and the black below. Posteriorly, they gradually merge with the color of the upper body. The ears are black with wide (to 17–18 mm) white edges along the upper margins. This edging is well marked against the black area of the facial band. Claws are dark-horn with yellowish cast.

Summer fur is much shorter, coarser and sparser. Length of guard hairs along the back is more than 50 mm. On the venter, hairs are particularly sparse and in places, the skin is visible through them. Color of badgers in summer is darker and more dirty dorsally, with yellowish or ocherous tinge; black tones ventrally are not as deep, but brownish. Yellowish tinge of the fur is determined by the corresponding color of the guard hair tips.

In the badger, there is one molt, extending the whole summer. New hairs attain their full growth only in hibernation. Therefore, summer fur is actually old being replaced and newly growing. General tone depends in part on wear and dirtiness of the fur.

822

Individual variation in badger color is quite obvious. Equally with several predominantly moderate "gray" types, there occur lighter and even very light animals generally of an almost silvery color. More frequently observed is a more or less significant darkening of general color tone of the dorsum, or the appearance on it of yellowish tones, giving the whole skin clayey highlights. Changes in intensity of color of the black bands on the head occur, and also the clarity of the white tone, which may be darkened. A brown tint may appear along the black ventral fields. According to some data, in each locality two color types are present—lighter and darker. Mention of color dimorphism in this species (Stroganov, 1962) is, however, without foundation. It is ordinary fluctuating variation.

Among sharp mutational changes, melanistic, albino and erythristic forms are known, and badgers of yellow color (Neal, 1948).

Sexual differences in color are absent. Newborn animals are covered with short white fur; in slightly older animals, fur is lighter than in adults. By the first hibernation, young animals don adult pelage. With increasing age, white portions of the hair increase in badgers, they lighten, and may even become very light.

Geographic variation in color is considerable and, it appears that relative to the described color types, it lies in somewhat weak lightening on one hand, and in strong darkening on the other. In the latter case, color may attain a brown tone, while light fields of the head become so dark that facial bands become poorly visible.

The extent, form and location of black facial bands change also. In some forms, they do not cover the whole base of the ear, but pass below it, usually only touching the inner margin of the ear conch base, and usually are narrower.

The skull (Middle Russian badgers) is quite massive and heavy, noticeably elongated and, if crests are disregarded, quite even in outline, not angular and moderately high.

The line of the dorsal skull profile, if the sagittal crest is not considered, is convex, with the highest point in the interorbital region. From this point, the line of the facial part descends at an obvious angle. Even steeper is the profile of the nasal opening. Posterior from the interorbital constriction, the profile line forms a very gentle arch, but descending more strongly in the occiput. The braincase is moderately developed, not swollen and not elongated, rounded-oval in outline, while the facial part of the skull is elongated and relatively narrow.

Zygomatic arches are narrow anteriorly and widely separated posteriorly, with their greatest width at the level of the articular condyles. Zygomatic width is considerably more than mastoid. The arches themselves are strong and massive, curved upwards in their posterior parts. The postorbital constriction of the skull is well-developed, but short and not sharply defined, and the skull width here is slightly less, equal or almost equal to interorbital width. In very old individuals, a fairly sharp intersection is formed here. Supraorbital processes are short, but well developed, sharply outlining the orbit, the dimensions of which are relatively very small. Its greatest diameter constitutes slightly less than half the interorbital width. The orbit opens posteriorly, but bone borders more than half its circumstance.

The hard palate, especially that part lying behind the toothrow, is long and narrow. Width of the palate between the inner margins of the molars is approximately 3.5 times less than its length from the anterior edge of the sphenopalatine notch to the alveoli of the middle incisors. The interpterygoid groove limiting the palate posteriorly is short and wide. Its length is only slightly more than the distance between the ends of the hook-shaped processes. The tympanic bullae are of irregularly angular (triangular) form, slightly swollen medially and moderately compressed (flattened) laterally. They do not contact the articular process. Mastoid processes are strongly developed and form massive outgrowths behind the

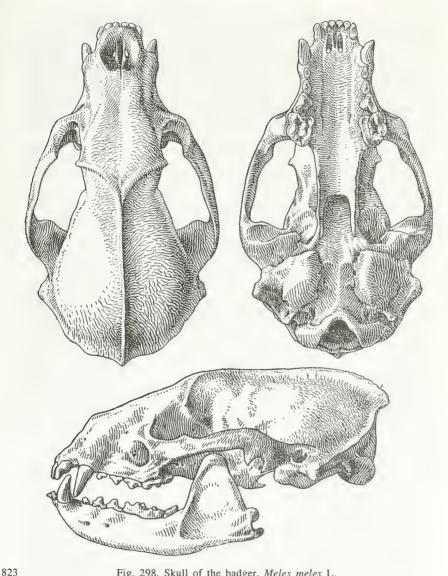


Fig. 298. Skull of the badger, Meles meles L.

auditory tubes which open independently of them. Paroccipital processes are short, triangular in form, their bases in contact with the posterior parts of the auditory bullae. The longitudinal diameter of the nasal opening is greater than the transverse. Infraorbital foramina are very large, irregular oval-rounded in outline. Their vertical diameter is equal to the diameter of the canine or greater than it: its greatest diameter is approximately half the diameter of the orbit.

Sagittal (arrow-shaped) and occipital crests are strongly developed—in old males, the height of the sagittal crest may be equal to half the interorbital width and even more. This crest reaches its greatest height in the middle of the parietals, arching downward posteriorly, and its end overhangs the occipital crest and occipital region in the form of a hook.

The lower jaw is relatively light and elongated; its ramus is almost straight; jaw height in the middle part constitutes about one-third the height in the region of the coronoid process. Posterior to the dental region, the lower line of the jaw profile rises upwards quite abruptly. The angular process is thick and short, the coronoid, broad and high—its height above the level of the articular process is almost equal to its width at this same level. The posterior region of the lower jaw has a low longitudinal crest ventrally.

Sexual dimorphism in the skull is insignificant and, besides dimensions, is manifested in somewhat less development of crests and generally somewhat "infantile" appearance of females. In young animals, the braincase is more swollen, postorbital constriction less marked—its width not less, but equal to or even more than interorbital width (in the very young animals, it is distinguishable), protuberances, etc. of skull are weakly defined, crests are not developed or only beginning to form. Complete development of the skull is, apparently, attained in the second year, although fusion of sutures begins earlier.

Geographic variation in the skull, not counting the size, is either weakly manifested or almost absent. There is some change in predominating form of the infraorbital foramen, in part (sculpturing) of the skull.

The upper carnassial tooth is relatively small, in plan, triangular outline (not pointed)—its length approximately equal to its width. Along the outer side, it bears one tall cutting cusp. The first molar is strongly enlarged in dimensions—its area is not less than the second, and greater than the area of the carnassial. It is rhomboid in form with parallel outer and inner sides, the main diameter lying approximately along the line of the toothrow; its inner side is greater [longer] than the outer. The tooth carries some low cusps, from which the two main ones are located along its outer edge and one lies more or less in the middle of its cup-shaped crown.

The lower carnassial tooth is large, strongly pointed, with three well developed apices in the anterior part and with an elongated flat and concave posterior part ("heel"); in length it exceeds the anterior part. The small premolars (one upper and two lower) are of the cutting type. The very small first upper premolar is easily lost and is frequently absent in adults, its alveolus is also not evident. The first lower premolar may also disappear and the

dental formula
$$I = \frac{3}{3} C = \frac{1}{1} P = \frac{4}{4} M = \frac{1}{2} = 38$$
 becomes $I = \frac{3}{3} C = \frac{1}{1} P = \frac{3}{4} M = \frac{1}{2} = 36$

or even $I = \frac{3}{3}C = \frac{1}{1}P = \frac{3}{3}M = \frac{1}{2} = 34$ or perhaps asymmetrical. With aging,

the upper molars may be more flattened as a result of wear of its apices.

Loss of the first premolar in different parts of the range occurs in different percentages of individuals (geographic variation). The same is true with the lower premolar; in a portion of the races, it has two roots, and in another—one.

The os penis is almost straight, with the dorsal side slightly concave or somewhat curved in an arc, and oval in cross section. At its tip, it is strongly widened in the form of a spoon and pierced in the middle with a small foramen elongated in the longitudinal direction. The sharp hook-shaped bend of the anterior end characteristic of the subfamily of martens, Mustelinae, is not formed.

Body length is 600–900 mm,² tail length 120–240 mm, length of hind foot, 75–130 mm, height of the ear is 35–70 mm.

Condylobasal length of male skull is 113.0–144.0 mm, of females, 100.0–140.0 mm; zygomatic width of males is 68.0–90.0 mm, of females, 62.0–85.5 mm; interorbital width of males is 25.2–34.5 mm, of females, 22.0–33.0 mm; postorbital width of males is 19.9–27.5 mm, of females, 18.1–26.2 mm; mastoid width of males is 55.9–71.9 mm, of females, 52.3–67.0 mm (from approximately 300 males and females of the Z[oological] M[useum of] M[oscow] U[niversity] and Stroganov, 1962, Siberia).

Os penis length is 72-76 mm.

²Body length of "about 90 cm" was stated by Ognev (1931) as the average length of old male badgers in Moscow province. The majority of authors refer to this length as maximal. Only Kuznetsov (1952) refers to greatest length of European badger as 105 cm, while Kashchenko (1900, 1902) stated that the greatest length of the Transbaikal badger is more than 100 cm. These data are, apparently, somewhat exaggerated, although the length of 90 cm is possibly not maximum.

Weight of badgers at the time of their active life changes very greatly, growing from spring to autumn, and reaching its maximum entry into hibernation. The badger accumulates very much fat, and relative to its general dimensions, its weight is disproportionally great. Average weight in autumn of badgers in the European part of the country, the northern Caucasus and Siberia is about 16–17 kg; a few large and particularly fattened animals reach 20–24 kg in weight; reports of badgers of 30 kg (Siberia; Stroganov, 1962) and 30 and 34 kg (Moscow and Ryazan districts; Ognev, 1931) are not reliable.

Weight of the Middle European badger in summer is 7–13 kg, in autumn 15–17 kg and as an exception—20 and perhaps even 25 kg (Gaffrey, 1961). Average weight of English male badgers is 12.2 kg, females somewhat less. The maximum established weight of males is 19 and 19.5 kg and of females is 17.2 kg. There exist unverified reports of animals of 20.4 and 22.6 kg in weight (Neal, 1948).

Females are somewhat smaller and lighter than males. Dimensions and weight of badgers vary somewhat geographically. Although these changes are not very sharp, extreme forms (Middle Russian—Amur, for instance) differ considerably (V.H.).

Systematic Position

Only species in the genus.

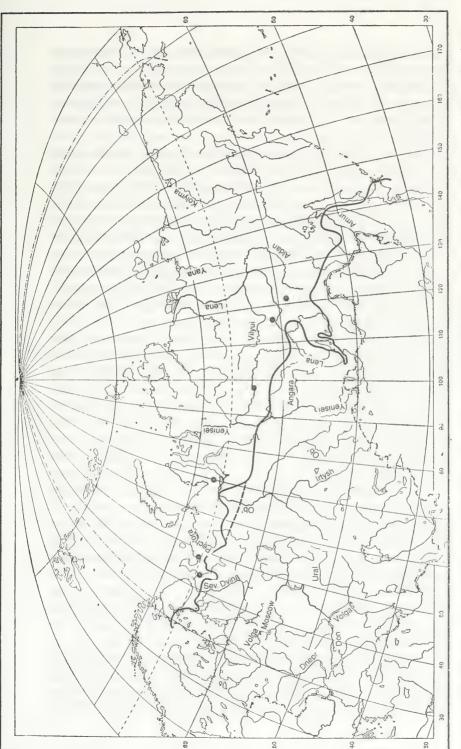
Geographic Distribution

Europe, Near and Middle Asia, southern and middle zones of Siberia, the southern Far East, China, and Central Asia.

Geographic Range in the Soviet Union

This constitutes a considerable part of the species range—its northern half and part of the western, and occupies the greater part of the country.

In the northwest, the northern border of the range begins in "the southwestern corner of Russian Laplandia" (Pleske, 1887): here, apparently the following is understood as districts to the west of Kandalaksha on the south, including Kuusamo (presently—Kusamo, in Finland). This is apparently the most northernly habitat of the species in Europe, lying at about 67° N. lat. On the Kola Peninsula, the badger is absent, but to the south of Kandalaksha,



of permanent inhabitation. The large dots designate distant, places of occurrence of the animal, possibly, transgressions, which are remote from 826 Fig. 299. Northern border of distribution of the badger, Meles meles L. in the USSR. Dashed line in the Trans-Urals is probably actual region the main distribution area. Counting from the west-Mezen', mouth of Pesha, Khal'mersede, mouth of Taimur, 150 km south of Suntar on the Vilyui, Kudu-Kyuel' on the Olekma. V.G. Heptner.

it is encountered all over Karelia and in particular, recorded at Ruvozer (Marvin, 1951, 1959). Thence eastward to Arkhangel'sk, the southern coast of the White Sea forms the northern border of the range. On Solovets Islands the badger is absent, and it is not known whether it occupies the northern parts of Onezhsk Peninsula.

On the eastern coast of the White Sea (Zimnii [winter] coast), the northern border of the badger's range begins north of Arkhangel'sk, slightly above 65° N. lat. (Shil'dlog village or farther north). Thence, it passes eastwards along this latitude to Kuloi and farther to Mezen' [still] on 65° N. lat. (Leshukonskoe village). Between Kuloi and Mezen', the border gives a sharp sag to the south—a narrow extension—descending to Karpogar on the Pineg [river]. From Leshukon on Mezen', the range border directs itself to the northeast along an irregular line and reaches the region of the source of Pesha river, flowing into Cheshsk gulf. This [point] is only 50–70 km south of the Arctic circle.

From here, the range border turns sharply to the southeast and, proceeding somewhat to the southwest of Ust'-Tsyl'ma on the Pechora, it goes to the middle course of the left tributary of the Pechora—the Izhma river south (about 70–80 km) of Izhma city. Thence, rising somewhat to the north, the border passes to the [main] Pechora at 65° N. lat. (data of V.Ya. Parovshchikov for 1962). Farther, the border goes to the Urals, apparently along this same latitude (Narodnaya mountain) or a little to the south—to Lyapinsk Urals (Flerov, 1933).

It is possible that, in the European part of the country, the range of the badger extends in some places even more to the north. Thus, a badger was caught at Kuloi near Kar'epol'e (50–60 km more south of Mezen' city; Zhitkov, 1904) and near Mezun' city (southern border of forest-tundra; Parovshchikov, 1959) and even on the coast of Cheshsk gulf near the mouth of the Pesha (forest-tundra; Parovshchikov, 1959). In these places, the character of the occurrence of this animal is not entirely clear, and the available data require more precision. However, it is evident that this far penetration to the north is connected with river valleys.

In western Siberia the badger was recorded near Salekhard on the Ob' at the Arctic circle (Stroganov, 1962; the most northern point of occurrence in Siberia). The border sinks sharply to the east and passes through the extreme upper reaches of the Pur and Taz (about 63° N. lat.; Yanushevich and Blagoveshchenskii, 1952*). It is possible that the actual northern border in the Trans-Ural lies somewhat farther to the south—near Berezov on a little lower (about 64°; Yanushevich and Blagoveshchenskii, 1952**) and corresponds more closely to the situation of the border in the Urals and eastward from the lower Ob'. The Berezov—upper Pur and Taz is nearer to the permafrost border. It is possible that its distribution to Salekhard is a distribution just along the Ob' valley. However, on the other hand the animal was noted at Khal'mersede north of the Arctic circle (Leble, 1953)³.

From the region of Taz sources, the border, going eastward, descends to the south and crosses Yenisei, somewhere at about 61° N. lat. At this latitude, or a little north, it goes into the basin of Podkamennaya Tunguska where the badger is met with at Baikit—at the mouth of Chunya in Tunguska (appr. 61° 35′: N. Naumov, 1934) and a little eastward on the Mutorya river (Podarevskii, 1936). It is entirely possible that the actual border of the range on the right bank of the Yenisei proceeds more to the north—the animal was noted (apparently transient) at the mouth of the Taimura river in Nizhnaya [lower] Tunguska (N. Naumov, 1934; this same place is sometimes referred to as the mouth of the Vivi river—both rivers flow into the Tunguska at nearly the same place).

828

Farther to the east, information on the limits of badger distribution are very few. Apparently, the border first directs itself towards a left [bank] tributary of the Lena—the Ichera, then extends somewhat northeastward (perhaps along the Lena valley) to the mouth of the Vitim (about 59° 30′ N. lat.; Maak, 1851; D. Ivanov) and even to a point about 150 km farther south of Suntar on the Vilyui (D. Ivanov, about 60° 40′ N. lat.). This place lies on the Lena or very close to it. In the latter case it is, very likely, always found as a transient since it is very distant—to Kudu-Kyuel' village on the Olekma is approximately 115 km in a straight line

***Misspelled "okhvatyvaet", instead of "obkhvatyvaet" in Russian original —Sci. Ed.

^{*&}quot;1958" in Russian original-Sci. Ed.

^{**&}quot;1953" in Russian original-Sci. Ed.

³The border in western Siberia is generally poorly clarified, and information is, in part contradictory. Thus, the earlier data (Slovtsov, 1892; Chugunov, 1915) speaks of its distribution in "Surgut Territory" and not north of 62° N. lat. in Surgut region on the Ob'. According to I.P. Laptev (1958), the northern border of the range, beginning at Berezov, embraces*** Kazym and passes somewhat to the south of the sources of Pur and Taz, reaching the Yenisei river at the mouth of Podkamennaya Tunguska.

from its confluence with the Lena (D. Ivanov). Transgressions to the two above-mentioned places and in part to the mouth of the Vitim are very rare—3 cases during 40 years (D. Ivanov).

From the mouth of the Vitim, the border curves, apparently arching a little towards the east, including the Bodaibo region, and turns back towards the southwest, apparently passing to the Kirenga river (to the west of Baikal) without reaching the northern extremity of Baikal and somewhere here, it reaches the shore of the Lake (from data of V.V. Timofeev)⁴.

In Trans-Baikaliya, the outline of the range no less complicated than to the west and north of [Lake] Baikal. The border in this region does not, judging from everything, extend so far to the north. Starting, apparently, on the shore of Baikal somewhere around the mouth of the Barguzin [river], it passes along the eastern slope of the Barguzin range on the northeast, crossing the Barguzin [river] at approximately 55° N. lat. and turns abruptly back to the south or southeast, including the Ikatsk range lying along the left bank of the Barguzin and just fails to reach the sources of the Ok' (tributary of the Uda—about 53° 30′ N. lat.).

Thence, the border bends sharply to the east and northeast, crosses the Vitim [river], proceeds through the region of the Amalat headwater—a tributary of the Vitim—(in its bend) and extending northeastward, passes somewhere south of the Kalar—in all events including the sources of the Olekma and its tributary, the Tungir; *i.e.*, nearly reaches 56° N. lat. (V.V. Timofeev, S. Anashkin). Therefore, apparently, the range beyond Baikal envelops the Vitim plateau, or at least a part of it.

From the above description, it follows that that part of the range located in the upper Lena north of Baikal (Bodaibo) is not directly united with Trans-Baikal. Not excluded is the possibility that such a complex picture of the northern range border in the Baikal region is formed on account of a deficiency of accurate data. However, it is most probable that this is the actual situation, and it is explained by the fact that the badger bypasses to the north and south of the northern Baikal and Stanovoi highlands, the southern and northern Muisk ranges and several ridges connected with them (Kodar, Udokan).

⁴On the map of Stroganov (1962, p. 162), the occurrence of badger northeast of Baikit on the Podkamennaya Tungaska was mentioned. This is, apparently, an incorrectly plotted habitat on the Mutorga river.

In Yakutiya, the badger is apparently not a permanent member of the fauna. It is known only from previously mentioned transgressions to the mouth of the Vitim south of Suntar village, and at Kudu-Kyuel' village on the Olekma river.

From that place on the upper Olekma in Trans-Baikaliya at about 56° N. lat. the border goes southeast, south of the Gilyui (Gassovskii, 1921) approximately through Solov'evsk to Zeya city and then to the middle course of the Selemdzha. Thence, it descends still more steeply to the southeast—to upper Burei, a little below the mouth of the Niman and in the source of a tributary of the Burei—the Tyrma. Farther along the Evoronsk lowland the border ascends towards the northeast, to the middle course of the Amgun', and then proceeds again to the southeast, crossing the Amur and reaching the ocean at 52° N. lat. (from materials of A. Samsonov and V.P. Sysoev).

On Sakhalin, the badger is absent.

To the south of the above-mentioned line in the European part of the USSR, the badger is encountered to the state frontier and beyond it. It is also all over Siberia. In Middle Asia, the badger is met with throughout the mountains and is only absent in individual localities, mainly in extreme high-montane regions. Thus, the animal is apparently absent in the high-montane Pamirs, most notably in the western [Pamirs]. Badgers do not, however, avoid deserts. In the Kyzyl-Kum, they are encountered at least along the edge; they are also recorded in the Ust'yurt, at least the eastern [Ust'yurt] (Bazhanov, 1951) and along the lower Amu-Dar'ya (Gladkov and Nikol'skii, 1935).

In Turkmenia, the badger lives mainly in montane regions, occupying in particular the whole of the Kopet-Dag and Bol'shoi Balkhan and, apparently, the Gyaz'-Gyadyk mountains (left bank of upper Tedzhen), Kushka valley and mountains to the east of Kushka (Chengurek mountains), and over the expanse lying along the mountains (V.G. Heptner). In the Karakum, the badger is rare, but is, apparently, met with almost everywhere (Yu.F. Sapozhenkov).

There are some unclear points and contradictions in the characteristics of the northern border of the range sketched above, and compared to several other works, may be explained not only by incomplete information and imprecision concerning transgressions of animals, and by natural fluctuations of the border during severe

829

conditions in the north of the continent.⁵ Apparently the badger, like some other species, has expanded its range northward in the last decade. Thus, according to relatively recent information (Parovshchikov, 1959), the northern border in the European part of the country shifted from Arkhangel'sk to Karpogory on the Pinega, thence to the upper Mezen' (Koslan) and across the middle course of the Izhma to the right tributaries of middle Pechora—the Shchuger* and Podcher'e. The border therefore passed considerably to the south of 65° N. lat.

Geographic Range outside the Soviet Union

The range occupies Europe, to the west including England and Ireland, and to the south to the coast of the Mediterranean Sea. It is on the Balearic Islands, Corsica, Sardinia and Sicily, as well as on the islands of the Aegean Sea except Rhodes, and, apparently, on Cyprus, the badger is absent; it exists in Crete. The northern border of the range in Europe begins on the Atlantic coast of Norway at Trondheim Fjord (about 63° 30′ N. lat.; Ekman, 1922) and, describing an arc, curves northward (to approximately 64° 30′ N. lat.) reaching the Baltic coast about the latitude 63° N. lat. In Finland, the border begins on the Gulf of Bothnia approximately at Raahe (about 64° 40′), and beyond forms a bend to the south, but in the east of the country again rises somewhat northward and nearly reaches 66° N. lat. (perhaps even as far as Kusamo; see above).

In Asia, the range occupies all of Asia Minor, Syria and Palestine, Iraq (apparently, only northern), northern, northwestern and western Iran (except the extreme south and the belt adjacent to southern Iraq) and northern Afghanistan. It may penetrate, perhaps, the territories connected with the Hindu Kush, to the more southern parts of the country contiguous with Baluchistan. In the east, the range extends to Kashgariya and Dzhungariya (details unknown—it is apparently absent in deserts); the entire northern half of the Mongolian Republic, southward including the Mongolian Altai, Khangai, Kentei, and sections lying to the south of these montane parts of the country, the extreme east of it. In China, the range occupies the entire western part of the country—from former

⁵In Arkhangel'sk district, after cold winters with much snow and late springs, the number of badger falls sharply (V.Ya. Parovshchikov).

^{*}Misspelled "Shchugor" in Russian original-Sci. Ed.

Manchuria to the extreme south. The range apparently extends to the extreme north of Vietnam—north of Hanoi. In the east, the range in China everywhere reaches the Pacific Ocean or to the borders of our country; its distribution to the west is not clear. It occupies Inner Mongolia, Gansu, Shanxi, Sichuan and, apparently, Yunnan or a part of this province (the opinion that badger are absent from this region has little basis), and possibly, the extreme north of Burma (information of its occurrence in Arakan between latitudes 20 and 15° N. is erroneous).

According to some data, the range also includes Tibet. In actuality, it does not, apparently, occupy all of this territory, which is less suitable for the badger's life, and occupies only a part of it—perhaps the southern and southeastern margins. Thus, the Chinese race was noted in Lhasa and Dzhangdze (Gyantse), southwest of Lhasa, and the plains north of Sikkim (Pocock, 1941). Perhaps the "Tibet" range extends through southwest China and Upper Burma as a projection eastward along the Brahmaputra valley and regions connected with it possessing relatively more favorable natural conditions. The range does not penetrate adjacent India (or Nepal) but the possibility of penetration of badger from the northwest southward to Chitral, and from the north to Baluchistan is not excluded. The range area also includes Japanese Islands⁶ and Korean Peninsula (V.G.).

Geographic Variation

Racial variation in the badger is considerable. It manifests itself both in amplitude of change in several characteristics and in the number of existing forms. About 40 names have been given to the badger and 24 subspecies are usually accepted, of which 11 are within our country (Ognev, 1931; Ellermann and Morrison-Scott, 1951; Stroganov, 1962). This number is evidently too great. Together with that, those attempts to revise the racial composition of the species that have been done do not reflect the actual situation and themselves represent an extreme in the opposite sense—4 forms for our territory (Novikov, 1956) and even 4 races for the whole species (V. Petrov, 1953).

⁶It is sometimes claimed that it occurs on Hainan (Pocock, 1941; Tate, 1947). This error is apparently based on a misunderstanding. Pocock (1941) offered data of Delacour about its occurrence "in the foothills north of Hainan". The last word is a misprint for "Hanoi". This text was so used above.



830 Fig. 300. Head pattern of various race groups of badgers—above, European badger, group meles; middle—"sand" or Siberian—Chinese, group arenarius—leptorhynchus; below, Far Eastern, group amurensis—anakuma. Sketch by N.N. Kondakov.

Geographic variation of badgers reveals itself in general dimensions, skull measurements (for the most part insignificant), form of the infraorbital foramen (a character not very well defined and permanent), form of the upper molar—its relative width (as well), structure of roots of the second lower premolar, relative frequency of loss of first premolars, general color tone and in form of head pattern. Color characteristics are most stable, typical and distinct. There are some geographic peculiarities in individual details of skull structure.

According to color type, all races of badger are clearly divisible into three groups. The remaining characteristics more or less agree with coloration. Races directly "intermediate" are absent; however, several other characters create "transitional" features in separate populations.

1. Group *meles*, European badgers. General color quite light and pure gray, "silvery"; sides of body a little lighter than middle of back. A wide black, rarely black-brown, stripe passes through eyes and envelops ear above and below (entire base of ear pinna). A pure white stripe passes from nose between [black] bands across forehead, behind ears and along neck. Cheeks and sides of head white, the white stripe passing along sides of neck⁷. Upper molar relatively wide—ratio of length to width less than 1:5; second lower premolar usually with two well-developed roots, first upper and lower premolars for the most part retained. Infraorbital foramen usually more elongated in vertical direction. Dimensions large to moderate.

In Europe eastward to the Volga, Caucasus, Near East, south and southeast Middle Asia.

2. Group arenarius-leptorhynchus, Siberian or "sand" badgers⁸. Color lighter, but in some forms, color corresponds to that of preceding group, and sometimes even darker, smudged with ocherous and brownish highlights. Sides a little lighter than middle of back. Dark facial stripe usually not black, but brownish in tone; it narrows behind eye and extends above ear. It does not go far posteriorly, sometimes hardly reaching ear. White color on head

 $^{7}\mathrm{This}$ type of coloration was described above in more detail in the section "Description".

⁸Animals of this type were recorded in our country for the first time from the Ryn sands between the lower Volga and Ural [rivers]. The form described from there by Satunin was called *arenarius*; *i.e.*, sand. This Russian name was introduced in our literature for the entire group of races, although the majority of them have no relationship to sands (montane, forest).

usually dirtyish. Light stripe passing along head dorsally between dark stripes relatively narrow and short; it does not extend behind ear or only extends behind it for a small distance and already merges with color of dorsal body on occiput.

Upper molar relatively elongated—ratio of length to width 1.5 or nearly that; second lower premolar usually with one root; first lower premolars for the most part absent. Infraorbital foramen more extended in horizontal direction. Dimensions moderate.

In Trans-Volga; Siberia except Amur region and Ussuri basin; Middle Asia except extreme south and southeast; and all remaining areas of Asia except Near East and notheastern China (former Manchuria) and Japanese islands.

From a zoogeographic and systematic point of view, it is noteworthy that in Europe, the Volga, and in part, the Kama (lower course) rivers separate two sharply differentiated race groups— European and sand badgers. They evidently play the role of an insuperable mechanical [physical]* barrier for badgers—animals which in these latitudes are not active in winter. This fact has multiple significance both in several general respects (problem of barriers, problem of clines, and others). If in some forms (see below), individual "transitional" characters are noticed, they do not apply to facial pattern. At the same time, the limits of distribution of both groups of badgers in the northeastern European part of the country, and in the northern Ural region are not clear. In the Pechora-Ilych preserve (upper Pechora), the Siberian badger exists. In Tien-Shan (see below), the races of both groups also approach each other closely, but are sharply separated by mountain ranges.

3. Group amurensis—anakuma. Far Eastern badgers. General color very dark, with brown tones strongly developed. Head pattern corresponds to that of the Siberian badgers; however, head dark, and dark stripes weakly defined.

Upper molar is elongated, second lower premolar with one root, first premolars always absent. Infraorbital foramen wider in transverse direction. Dimensions small.

In Amur region, Ussuri basin, northeastern China (former Manchuria), and Japan.

Badgers of groups 1 and 2 were, up to the 30's, considered different species—M. meles and M. leptorhynchus (Ognev, 1931).

^{*}In Russian original, the word mekhanicheskoi is used-Sci. Ed.

The Amur-Ussuri badgers were affiliated with the latter. The recent attempt to restore this completely neglected point of view (V. Petrov, 1953), was naturally unsuccessful.

The scheme of races given below is preliminary.

832

Group of European badgers, meles.

1. Middle Russian badger, M. m. meles Linnaeus, 1758 (syn. tauricus, caucasicus).

Dimensions large.

Color of back relatively pure silvery-gray tone. Main tone of head pure white, dark stripes wide, black in color, white fields extend far backward along upper and lateral parts of neck. Pelage relatively soft with relatively dense underfur.

Skull with strongly developed crests, second lower premolar with two separate or merely adjacent roots; first premolars, often all, usually present; upper molar relatively wide—ratio of length to width about 1.25, and usually not more than 1.35. Infraorbital foramen extended in vertical direction, and its greatest diameter, being directing upwards and somewhat internally, greater than transverse diameter.

Dimensions maximmal for its group; apparently, for entire species. Middle Russian badgers are largest—they are, evidently, larger than Middle and Western European.

Condylobasal length of male skull is 125–140 mm, of females, 123.2–133.6 mm; zygomatic width of males is 75.2–89.5 mm, of females, 68.0–85.2 mm; mastoid width of males is 62.1–71.9 mm, of females, 58.5–67.0 mm; length of upper molar of males is 14.7–17.1 mm, of females, 14.5–17.1 mm; greatest width of posterior molar of males is 11.2–13.2 mm, of females, 11.0–13.5 mm (Ognev, 1931; some deviation in both directions possible). In animals of this race, different numbers of first premolars retained in different parts of range—in Middle and Northern Russia, only 77%, in the south—60%, in Cis-Caucasus—66%, and in Crimea—about 72% (V.G. Heptner).

Weight up to 20–24 kg (autumn), in exceptional cases, perhaps a little more (see above).

In European part of Union eastward to Volga, in the Crimea, Cis-Caucasus and northern Caucasus. Distribution to east in north

⁹The above-given description (page 1234) applies to this form.

of European part of country not known (see below, separation from Siberian badgers).

Outside the USSR, in remaining parts of Europe except Rhodes, Crete, Spain (existence of a separate race in Denmark is unlikely).

Badgers from the northern slopes of the Caucasus, its foothills and adjacent plains may be, on average (skull dimensions) slightly smaller than Middle Russian. In this one might see some tendency toward transition to the Trans-Caucasian form. This difference is, however, completely insignificant and separation of a different form, caucasicus, is not justified.

2. Kizlyar badger, M. m. heptneri Ognev, 1931.

Dimensions large (as in the preceding form).

Color very pale, dull, dirty-grayish-ocherous. Black stripes on head narrow, but typical of European group.

Skull as in preceding form.

In Caspian steppes area (steppes of northeastern Cis-Caucasus), right bank of lower Volga (Kalmytsk steppes), and Volga delta.

Outside the USSR—absent.

A very poorly known form; exhibiting several characters similar to the Siberian badger group, but on the whole typical of European [group]. Range is very small, especially as compared to other subspecies, but on the whole, characteristic of a series of mammalian races, mainly of eastern origin, which are also restricted in their distribution to the above-mentioned section of steppes, deserts and semideserts.

This form requires further study and here is provisionally recognized.

As yet there is no basis for placing it in synonymy with the nominal form.

3. Trans-Caucasian badger, M. m. canescens Blanford, 1875 (syn. minor).

Dimensions smaller than preceding forms.

General color of dorsal side dirtyish-gray with highlights of brown tones. Head color as in nominal form. Skull and tooth structure as in nominal form; *i.e.*, infraorbital foramen high, but upper molar somewhat elongated, though not so strongly as in Siberian badgers, and crests somewhat more weakly developed.

Condylobasal length of male skull is 116.0-123.3 mm, of females, 111.8-122.0 mm; zygomatic width of males is 68.0-81.5

833

mm, of females, 66.0–72.0 mm; mastoid width of males is 56.0–63.2 mm, of females, 56.1–58.0 mm; length of upper molar in males is 15.9–17.3, its width 10.0–11.1 (Ognev, 1921). In badgers of this form, about 57% of possible number of first premolars are retained (V.G. Heptner).

In Trans-Caucasus, Kopet-Dag and apparently, Gyaz'-Gyadyk mountains (right bank of upper Tedzhen); probably elevated regions of Kushka (Chengurek mountains) in Turkmenia. Limits of distribution in northern Turkmenia not known.

Outside the USSR—in Iran, Afghanistan, and possibly Asia Minor.

4. Fergana badger, M. m. severzovi Heptner, 1940.

Dimensions quite small, apparently close to preceding form.

Color of dorsum relatively pure silvery-gray without yellow sheen or with only insignificant development of it. Black stripes on head wide occupying whole ear.

Upper molar short and broad; *i.e.*, typical of European badger group, preorbital foramen extended in transverse direction; *i.e.*, a character of Siberian badgers.

Condylobasal length of skull (10) is 109.4–M 118.4–127.0 mm; zygomatic width is 64.5–M73.2–81.6 mm. In animals of this race, the least number of the first premolars—about 26% of the number possible, among all groups of races (V.G. Heptner).

In region of right tributaries of Pyandzh and upper Amu-Dar'ya, Pamiro-Alaisk system (apparently, Eastern Pamir only; the Alaisk valley), Fergana valley and mountains bordering it on south and north (Chatkal and Fergana ranges).

Outside the USSR-absent.

The Fergana badger stands closest to *M. m. canescens.** However, it is substantially different from it, several skull characteristics "transitional" to the Siberian badger group in particular being most noticeable. It is probable that its range is separated from that of *M. m. canescens* by the Pyandzh [river]. There is a remarkably sharp boundary between its range in the north and badgers of the *leptorhynchus* group (sand) which occupy the northern ranges of the Tien-Shan system. Already along the southern slopes of the Talas Alatau south of Issyk-Kul, and along the upper Naryn are distributed typical representatives of the Siberian badger group. The limits between both forms in the plains are not clear. In all

^{*}See above, Trans-Caucasian badger-Sci. Ed.

events, M. m. severzovi was recorded in Kugitangtau (Ishunin, 1961), and M. m. leptorhynchus in Nuratau (Kuznetsov, 1948). Other data on badgers of Middle Asia are poorly defined, and partially contradictory (Kuznetsov, 1948; Ishunin, 1961).

Group of Siberian, or "sand" badgers arenarius—leptorhynchus

5. Siberian badger, M. m. sibiricus Kastschenko, 1900 (syn. altaicus, raddei, aberrans).

Dimensions moderate—somewhat smaller than in nominal form, but larger than in Trans-Caucasian.

General color tone of back light—gray, usually with yellowish or straw-colored and sandy-straw highlights. Dark stripes on head typical for group—narrow and extend along dorsum of head, not including ear. Their color varies from brownish-black to tawny-brown. Pelage long and relatively soft with dense undercoat.

Upper molar relatively elongated, ratio of its length to width about 1.5. Infraorbital foramen extended in transverse direction, second lower premolar with one root, and first premolars very rarely occur.

Body length of males (6) is 675-M720-750 mm, of females (4), 620-M668-692 mm; tail length of males is 185-M214-235 mm, of females, 174-M196-222 mm; length of hind foot of males is 100-M116-127 mm; of females, 82.0, M84.2-86.0 mm; ear length in males is 38-M39-41 mm, of females, 37-M38-40 mm.

Condylobasal length of male skull (7) is 123.0–M125.8–128.7 mm, of females, (5) 116.0–M117.4–118.7 mm; zygomatic width of males is 75.6–M78.0–80.5 mm, of females, 68.4–M69.2–70.2 mm; interorbital width of males is 27.3–M27.8–28.3 mm, of females, 26.2, M26.6–27.0 mm; postorbital width of males is 22.0–M23.8–24.6 mm, of females, 20.0–M23.2–24.0 mm; mastoid width of males is 64.0–M68.7–75.4 mm, of females, 58.6–M60.2–62.0 mm.

Percentage of retained first premolars differs in different populations of this race—in Bashkiria and southern Urals—about 13[%], in Siberia and Altai—3[%] and in Trans-Baikaliya—0[%] (V.G. Heptner).

Weight of adult males reaches 10-13.6 kg, and evidently even more (all data on dimensions after Stroganov, 1962).

In Siberia including Trans-Baikaliya and Altai, northern parts of Kazakhstan and probably northern Trans-Volga.

834

Outside the USSR-unknown.

The independence of the Siberian form of badger was sometimes, and is now, doubted. At the same time, its differences from the form *arenarius*, and from the Mongolian form *leptorhynchus*, is sufficiently real. Separation of this race is arguable, but the racial identity of, for example, badgers from the middle course of the Ob' and from the deserts and semideserts of southern Kazakhstan and Uzbekistan one may hardly admit even theoretically. Neither is the view by which all badgers from the Trans-Caucasus, Siberia and Turkmenia to Central Asia, China and Tibet belong to one form (Petrov, 1953; Novikov, 1956) acceptable.

The separation of the form *aberrans* Stroganov, 1962, demands confirmation. This form is, to a high degree, doubtful, both as regards its characters and its range ("northern regions of eastern Kazakhstan"—Tselinograd, Kokchetav, Pavlodar, Zaisan Lake and middle Tarbagatai).

Concerning Trans-Volga badgers, see the following form.

6. Kazakhstan or sand badger, M. m. arenarius Satunin, 1895. Dimensions moderate—somewhat less than in nominal form, but greater than in Trans-Caucasian form.

Color is lighter and paler than in northern forms, conditioned by decrease in black bands of guard hairs and their frequent full reduction on sides of body, where the color acquires a pale-straw tone. A clayey tone usually develops over the entire skin, which impinges on the silvery-gray color characteristic of northern races. Pelage is coarse, bristly and underfur is scarce.

Structure of skull and dentition as in Siberian badger, $M.\ m.$ sibiricus.

Body length of males (4) is 700-780 mm, of females (4), 610-700 mm; tail length of males is 200-220 mm, of females, 185-250 mm; length of hind foot in males is 115-126 mm, of females, 95-110 mm; ear length in males is 58-70 mm, of females, 40-80 mm (Sludskii, 1953).

Condylobasal length of male skull is 115.0–131.0 mm, of females, 109.0–118.0 mm; zygomatic width of males is 68.6–77.7, of females, 62.2–73.8 mm; mastoid width of males is 55.9–65.0 mm, of females, 52.3–58.8 mm; width of upper molar in males is 10.1–12.1 mm, of females, 10.1–12.3 mm; length of upper molar in males is 14.1–16.6 mm, of females, 14.0–16.0 mm. Percentage of retained first premolars—about two (V.G. Heptner).

Weight of males in March-May is 7.8-8.3 kg, in March-June is 5.6-7 kg. Weight of young animals in November is 10.5-12.5 kg, of an adult female, 14.5 kg (Sludskii, 1953).

In southern Trans-Volga (Volga-Ural steppe), Kazakhstan except the northern and montane parts, and plains of Middle Asia except the parts occupied by the forms *canescens* and *severzovi* (extreme southern Turkmenia, Pamir-Alaisk mountain system, Fergana valley and the mountain ridges bordering it on the north).

Outside the USSR—absent.

This described form of badger is morphologically and geographically well-characterized. Its distribution in northern Trans-Volga is not clear. It was recorded in the southern Urals (Kirikov, 1952), at the latitudes of Samarsk Luka and Bashkiria. However, these data indicate only the presence of badgers belonging to the "sand" group in these places, but they do not confirm its identity with the form *arenarius* from the Volga-Ural steppe and Middle Asia. This is all the more so, since badgers of northern Kazakhstan belong to the Siberian form *sibiricus*. It is possible that these Trans-Volga badgers (except southern) also belong there. In general, as was shown, limits of distribution of the sand badger group to the north in the Cis-Urals are not known to be contiguous with the *meles* group.

Information on the occurrence of this form in the steppes of the Cis-Caucasus ("Caucasian steppe", Ellerman and Morrison-Scott, 1951) was mistaken. As was shown, all of the forms of the *leptorhynchus* group are absent west of the Volga and Caspian Sea.

7. Tien-Shan badger, M. m. tianshanensis Huene, 1910 (syn. talassicus).

Dimensions moderate.

General color same as type, and as in Kazakhstan badger, *M. m. arenarius*, but somewhat darker, the yellow sheen is weaker or not developed, the fur longer, denser and fluffier. Percentage of retained first premolars is about 8.3% (including material from around Dzhungariya; V.G. Heptner).

In the northern ranges of the Tien-Shan including Dzhungarsk, Zailiisk, Kirghizsk and Talassk [Alatau]. In the eastern parts of the [mountain] system within the USSR, southwards as far as the upper Naryn [river].

Outside the USSR—probably in the Tien-Shan system in Dzhungariya and Kashgariya [China].

It is a completely unclear and entirely doubtful form which requires additional study and confirmation. It is to the highest degree close to the Kazakhstan badger, M. m. arenarius (many individuals are not distinguishable at all) and apparently, differ only in somewhat denser underfur, as is frequently the case with montane populations.

The southern limits of this form and the whole "sand" badger group requires more precision. The Fergana badger, M. m. severzovi (see above), exists along the southern slopes of Chatkal and, probably, Fergana ranges and Tien-Shan form along the upper Naryn.

Note. The problem of variation and nomenclature of badgers of the northern Tien-Shan is not clear. Hoiningen-Huene (1910) named the Tien-Shan form from living animals received from Hagenbeck* and caught in "Tien-Shan" but not noted whether within the borders of the [present] USSR or in China. From photographs and the description it is clear only that this is a typical "sand" badger. Ogney (1931), without attempting to precisely limit the type locality (t. t.** restricta) of the form tianschanensis, allo-836 cated to it individuals from the extreme eastern—Chinese—parts of the Tien-Shan (Kul'dzha, Kunges river, Kaitsalai, Yuldus, Boro-Khoro range). At the same time, he described the distribution of this form, according to data of N.A. Severtsov, in a series of places in the eastern parts of the Tien-Shan within the borders of the USSR westward to the Chu river as well as in the western Tien-Shan, "for the entire range in general" and even for the Karatau (page 478). Factually, therefore, it is to take the habitation of the form tianschanensis throughout the entire Tien-Shan, within the borders of our country and beyond them.

On a par with this, in the same work [Severtsov, 1873] (pages 478-479). M. m. talassicus was described from Talassk Alatau (southern slope) from two specimens; the occurrence of which is assumed to be also on the Chu river (Frunze-"Pishpek"***). Differences from the form tianschanensis given are very insignificant (somewhat darker color). The place of origin for M. m. tianschanensis has not yet been accurately established—and besides it is entirely doubtful—that it is possible that there are different badgers of the type arenarius-leptorhynchus from the different parts of Tien-Shan, there is no basis for admitting the independence of the form talassicus.

^{*}German animal dealers-Sci. Ed.

^{**}For "terra typica"; i.e., type locality—Sci. Ed.

^{***}Presently Bishkek, Kyrgyzstan-Sci. Ed.

Group of Far Eastern badgers, amurensis-anakuma.

8. Amur badger, M. m. amurensis Schrenk, 1858 (syn. schrenkii).

Dimensions very small, smaller than in the Trans-Caucasian badger M. m. canescens. It is the smallest race of the species.

General color very dark, darkest among all races. Dark stripes on head extend above ear and disappear in dark field of occiput; they are black or dark blackish-brown or sometimes coal-black in color. Entire area between stripes and cheek region, *i.e.*, places which in other races are white or very light, are dirty grayish-brown in color. It may be so dark that stripes are weakly distinguished or almost undetectable. Color of back very dark due to strong development of dark bands of the hairs, grayish-brown with silvery highlights, depending on white tips of hairs. Sides of body only slightly darker than back. Pelage with little wool, but soft.

Skull small, with smooth outlines, relatively light. Protuberances, etc. on skull weakly defined, and crests very weakly developed even in oldest individuals (wear on crown of carnassial teeth). Entire skull has infantile features. Infraorbital foramen extended in transverse direction, upper molar is elongated. First premolars always absent (extreme degree of reduction within limits of species).

Body length 60-70 cm.

Condylobasal length of male skull (6) is 111.0–117.9 mm, of females (6), 104.8–112.2 mm; zygomatic width of males is 67.8–75.4 mm, of females, 62.1–73.2 mm; mastoid width of males is 57.3–63.5 mm; of females, 53.0–58.2 mm; interorbital width of males is 24.0–29.2 mm, of females, 22.1–24.6 mm; postorbital width of males is 20.8–22.4 mm, of females, 18.2–21.9 mm (Stroganov, 1962 and materials of Z[oological] M[useum of] M[oscow] U[niversity]). Length of upper molar in males is 16.2–17.0 mm, of females, 14.0–15.3 mm; width of upper molar in males is 11.2–11.5 mm, of females, 9.6–10.8 mm (Ognev, 1931).

Badgers of this form are always characterized by complete absence of first premolars and corresponding change in dental formula (V.G. Heptner).

In Ussuri Territory and Priamur'e westward approximately to 123° E. long. (Albazin).

Outside the USSR—in contiguous parts of northeastern China (former Manchuria), and probably westward to include the Bol'shoi [Great] Khingan [range] and Korean peninsula.

The Amur badger is a sharply distinguished form. In its head pattern, it resembles races of the "sand" badger group, but is sharply separated from them and all other forms of the species by its saturated darker color, by size and complete reduction of all first premolars; *i.e.*, by dental formula. This form, undoubtedly, possesses features similar to the Japanese badger, *M. m. anakuma*; however, the union of both races is unfounded.

The borders of the range of the Amur subspecies are still not fully clear. There was some information that badgers of Trans-Baikaliya possess characters transitional to the Amur form, but this is not so. In the Mongolian Republic, near Beijing, and possibly in the central Manchurian plains lives a badger of the typical "sand" type, extremely light.

The Amur badger is a clear example of one of the characteristic features of geographic variation of some widely distributed species of Palearctic mammals—darkening or more saturation of color, and partly decrease in size in the south of the Far East (Cervus elaphus, Capreolus capreolus,* Mustela sibirica and several others).

* * *

Beyond the borders of our country, a quite large number of farms have been described. The independence of many, if not the majority, of them needs confirmation. Usually accepted are: 1) *M. m. anakuma* Temminck, 1844—Japanese Islands (Hondo [Honshu], Shikoku, Kyushu, ? Hokkaido); 2) *M. m. melanogenys* J. Allen, 1913—Korean Peninsula (evidently a synonym of *M. m. amurensis* V.H.); 3) *M. m. leucurus* Hodgson, 1847—southeastern Tibet (Lhasa); 4) *M. m. leptorhynchus* Milne-Edwards, 1867—China, Mongolian Republic¹⁰; 5) *M. m. blanfordi* Matschie, 1907—

*Now considered a distant species, C. pygargus—Sci. Ed.

¹⁰Osgood (1932) considers the forms *leucurus* and *leptorhynchus* identical. This point of view was, apparently, also supported by G. Allen (1938). In this case, the Chinese-Mongolian badger must be called *leucurus* (not *leptorhynchus* as accepted by Allen). In general, the identity of badgers from Lhasa and from around Beijing (the type localities of both forms) is very doubtful, and this question needs further study.

Allocation to *leucurus* of the badgers of Siberia, Middle Asia and even Trans-Volga (Bashkiria; V. Petrov, 1953) belong to *leucurus* is, of course, not accepted.

Kashgariya; 6) M. m. marianensis Graells, 1897—Pyrenese [Iberian] Peninsula; 7) M. m. arcalus Miller, 1907—Crete; 8) M. m. rhodius Festa, 1814—Island of Rhodes, Aegean Sea; 9) M. m. ponticus Blackler, 1916—Asia Minor (very probably, a synonym of M. m. canescens; V.H.); 10) M. m. danicus Holton, [1935]— Denmark (evidently a synonym of the nominal form) (V.H.).

Biology

Population. Badger populations within the limits of its range are variable. It is determined chiefly by the abundance of food, breeding burrow conditions and sources of drinking water. In the breeding period, in the large spruce swamps, and on the water divides of the Volga and Zapadnaya [western] Dvina, its density was not great, reaching 0.13-0.16 per 10 km². In the forest-steppe, in island of broad-leaved oakgroves (Tula abatis; Likhachev, 1956), average density over 13 years was from 1.6 to 2.1 per 10 km². In one of the great islands (28 km²) of the delta of Ili river in Kazakhstan (Sludskii, 1953), density reached a maximum of 21.0-26.0 per 10 km² (15-16 litters). Data on the number of inhabited burrows are less reliable: some burrows are only periodically inhabited and in others, up to three litters live (badger "city").

In the European part of the USSR, the badger is most numerous in the middle zone—there where islands of forests prevail, and the locality itself is hilly and cut with ravines. Thus, in Tatariya, 3-9 animals are found in 10 km² of wooded lands suitable for the habitation of badger (Gorshkov, 1964).

The greatest number of badger skins are obtained from Kazakhstan, although the animal itself is far from numerous throughout the region. The least number of badgers is in the northern Kazakhstan steppes. It is most numerous in Alma-Altinsk, Dzhambul and Chimkent districts (Sludskii, 1953). In the taiga, both lowland and montane, the badger is rare. The same must be said for the open steppes.

838 Habitat. The badger reveals great flexibility with respect to habitats. Just as in steppe and forest foxes, wolves, tundra and taiga reindeer, etc. badgers of various races differ in their ecology. The badger in the forest zone is a forest animal, mainly restricting itself to forest edges, forest islands, coppices and wooded ravines. It is most numerous in the zone of islands of mixed forests

alternating with fields, meadows and settlements. It avoids large forest massifs, rarely settling those, and if so mostly along edges; such forests have little food for them. On the contrary, in a small island forest of 15–20 h, there are sometimes up to three litters of badger. In some localities (Byelorussia, Kirov district), the population of badgers corresponds to the percentage of woodlands, which is explained by the excessive pursuit of the badger by man, and not by environmental conditions. In Moldavia (Korchmar', 1963), the badger inhabits the forest tracts of Kodra, in insular forests of the northern regions and in southern forests. It is most numerous in small islands of forest. For the badger, the forest is merely a good refuge sheltering it during foraging, and not a necessary surrounding for its life.

In the habitat, besides abundance of food, favorable burrowing conditions are the most important requirement. This is natural for an animal pursuing a semisubterranean way of life, in which the greater part of the [24 hour] day and several winter months are spent in the burrow. The badger prefers dry, sandy-loam soils with a deep ground water level for easily-yielding excavation. In extreme cases, it settles in more or less moist soils, choosing the most elevated, well-drained places. Forest attracts the badger not only as a shelter, but also thanks to the presence of the Ortstein horizon which is impermeable to water (Kolosov, 1935), under which it digs its burrows. For the same reason, it prefers sand lying beneath a layer of clay or loam. The water-impermeable upper layer of soil then serves it as the vault of its underground constructions (Lukhachev, 1956). The badger sometimes digs burrows in sands of pine forests, and also among rocks.

The second condition for the badger is the proximity of water, especially when the approach to it from the burrow is hidden. In open dry steppes of southeastern Trans-Baikaliya, habitats of the badger are always connected with water resources. In Kazakhstan, the badger sometimes makes its burrow not more than 5–10 metres from water (Sludskii, 1955). The badger does not avoid human settlements as long as the burrow itself is located in a little-populated, hidden place, most often on the slopes of a deep ravine overgrown with trees, bushes and tall grasses.

In the middle zone, the badger prefers the edges of mixed forests but it does not avoid coniferous forests. And here, it prefers sections dissected by ravines, but sometimes settles on flat plains.



839 Fig. 301. Montane oak and mixed coniferous-broadleaved forests. Typical habitats of Amur badger in southern Primor'e. "Kedrovaya Pad'" preserve. Here also exists a fauna complex of Ussurian Territory—kharza, racoon dog, white-chested bear, leopard, and others. July 1964. Photograph by A.G. Pankrat'ev.

In the forest-steppe zone, the badger more often burrows along the slopes of ravines and gorges which are very often covered, if not by forest then by steppe shrubs and rank growth of grasses.

In Kazakhstan, the badger is an animal of steppes and semideserts, ecologically different from the badger of the forest zone. In northern Kazakhstan, it settles along the slopes of ravines (saev), the high ridges near lakes in islands of pine woods, on high terraces, and along the river valleys. In central Kazakhastan, it settles in the bank precipices and the slopes of hills and ravines, especially the shores of lakes and rivers. In the desert zone, it lives in consolidated sand hills alternating with solonchaks, streams and lakes, in flood lands and deltas of rivers. Many badgers are also found on "terraces"* of foothills, especially in apple forests on the slopes of mountains. In mountains here and in the Caucasus it ascends to a height of 2300–2500 m. In the montane Altai, it restricts itself to the lower belt of the mountains—not higher than 1000–1200 m.

In Ussuri Territory (Yu.A. Salmin and V.D. Shamykin), the badger is associated with more gentle relief. It is encountered in valleys of large mountain rivers—in well-drained dry valleys at the foot of slopes.

Food. Of the whole order of carnivores the badger, like the brown bear, is the least carnivorous. In the badger as well, the development of powerful teeth and masticatory musculature is connected not with carnivory, but with omnivory. While in the pine marten with mixed feeding the intestine length surpasses body length by 4.5–5 times, in the badger it is 8 times (in the bear, by more than 10 times).

The badger's food consists of rodents (mainly voles), rarely small birds, amphibians (mainly frogs) and reptiles (mainly lizards), insects and their larvae, molluscs, earthworms, various fruits, nuts, berries and other plant food.

The species composition of food, and within it the ratio of each food type, is subject to considerable variation, both seasonal and geographic. The effect of geographic variation upon food composition can be judged by Table 70, which presents the data on the most important foods of 7 separate parts of the range. Actually, the diversity of the food components is still more significant. Apparently, in the northern parts of the badger's range there is more carnivory, less in the south where sources of its food are more abundant and varied (Crimea, Kazakhstan).

Among mammals, common and red-backed voles are the most important. The role of birds is not great. Usually, they are small birds nesting on the ground, mainly during the nesting period, or some kinds of wounded birds. The shores of large bodies of water

^{*}In Russian original "prilavok," or counter, shelf-Sci. Ed.



840 Fig. 302. Broad-leaved forest in the valley of Kedrovaya river—typical habitat of Amur badger "Kedrovaya Pad'" preserve, southern Primor'e. October 1963.

Photograph by A.G. Pankrat'ev.

constitute an exception (Kaletskaya, 1957). In destruction of eggs and young of game birds, badgers, for the most part, are accused without cause. In the forest zone, frogs are, in places, of great importance. In the dry forests of Zhigula, the importance of slow-worms [anguine lizards]* increases, while in the Buzulak pine forest—it is lacertid.

Among invertebrates in forests, of greatest significance are dung beetles, various ground beetles, stag-beetles, longhorn beetles, forest may beetles and june beetles and their larvae, sawflies, wasps and bumblebees and their larvae. The badger eats many mollusks (mainly slugs) and earthworms (in large amounts). Among plant foods, of greatest importance are acorns, hazelnuts, strawberries, wild apples, pears and others. In Kazakhstan, the main foods of the badger consist of insects, mainly mole crickets, and in some years—Asiatic locust on which it is quickly fattened (Sludskii,

^{*}The Russian word "veretenitsa" is applied to both Anguis fragilis and Coronella laevis—Sci. Ed.

J F -	Tula Abati: (Likhachev 1956)	, and	Zhiguli (P.B. Yurgenson	Buzuluk pine) forest (Shilova- Krasova, 1951)	Montane Crimea (Savina, 1940)	Ili river	Ryabinsk water i, reservoir (Kaletsk- aya, 1957)
Mammals	70.6	54.2	57.5	17.1	34.1	23.6	No data
Rodents	69.0	53.6	56.6	17.1	29.8	20.8	14.5
Birds	27.0	2.3	2.6	4.1	3.5	8.3	17.6
Bird eggs	3.2	2.1	_	_	2.2	12.5	15.3
Reptiles	4.0	0.6	8.8	22.5	_	31.9	24.6
Amphibians	26.3	8.6	_	-		_	88.2
Insects	96.0	76.8	86.7	95.4	98.0	94.4	97.0
Beetle larvae	17.7	18.4	17.7	36.9	9.3	0.6	
Molluscs		0.8	15.0	0.1	14.6	_	12.3
Plant materia	ıl 23.8	28.3	23.9	_	50.7	. 15.0	77.6
Sample size	126	474	113	221	224	144	134

1953). In the Crimea, among insects in the badger's food, ground beetles and stag-beetles predominate; a large role is played by fruits of dewberry, wild pear, apple, acorn, and beechnut. The badger also raids vineyards (Savina, 1940).

Seasonality of food types is conditioned by the degree of their abundance and availability, which is not the same throughout the year.

The seasonal changes in food composition of the badger in Moldavia are as follows (Korchmar', 1962; % occurrence):

First half of summe	er	Second half of summer-autumn			
(572 excrement samp	oles)	(226 excrement samples)			
Mouse-like rodents	18.3	Mouse-like rodents	67.5		
Subterranean voles	10.4	Small birds	7.5		
Stag-beetles	45.2	Ground beetle	10.0		
Ground beetle	45.2	Rose chafer	10.0		
Rose chafer	31.3	Beetle larvae	7.0		
Beetle larvae	33.3	Plum	65.0		
Sweet cherry [P. avium]	60.3	Dogwood	44.0		
Strawberry	12.9	Apple	10.0		
Pear	5.0	Grape	7.0		

In Zhiguli (P.B. Yurgenson), dung beetles are most frequently found in the badger's food in May, but in June—twice less; later they rarely occur. Land molluscs are most often found in July—August, as is hazelnut. Red-backed voles [Clethrionomys rutilus] and wild apples are utilized most of all in August. Mountain leafhopper larvae are more encountered in the badger's food in June, beetle larvae in June—August, and wasps (3 species) in July—August. All of this is associated in a very close way with the natural abundance of these foods.

It is characteristic for the badger that during one hunt it catches one food type predominantly, but in considerable amounts: thus, in

the stomachs of three badgers caught on 3 November, were 57, 63 and 75 frogs (A.N. Skorodumov); in one caught on 31 May—97 maybeetle larvae (Likhachev, 1956), on 27 May—65 maybeetle larvae and 50 dung beetles, on 26 September—285 gm of wasps and their larvae (P.B. Yurgenson), on 26 June—146 barbel beetle larvae, on 5 July—362 larvae of bumblebees, and on 22 August—152 earthworms (Likhachev, 1956). In Moscow district near Klin, during autumn, the stomachs of several adult badgers killed in the morning when they returned to the burrow after a night's foraging, were full of earthworms only, or with small terrestrial frogs only.

The latter were, evidently, taken from hibernating aggregations (V.G. Heptner). In Central Europe (Rörig)*, 9 old and 74 young voles and 7 frogs were found in one stomach, etc. In general, the badger most often eats not more than 0.5 kg food per day, and young (up to one year old), more than adults. Therefore, an adult

In the badger are clearly revealed differences in foods in different biotopes. Thus, in Tataria and adjacent regions, amphibians, gray voles, fish, briar, blackberry and orthopterous insects predominate in foods of animals living in water-meadows; in pine woods—maybeetle, click beetles, red-backed voles and blueberry; in broad-leafed forests—dung beetles, mouse-like rodents, earthworms and acorns (V.A. Popov). The significance of the badger in destruction of the harmful rodents and insects is quite noteable. In Tataria, in young pine woods, up to 60 thousand places dug by the badger were located, which here destroys up to 75% of all maybeetle larvae (Gorshkov, 1964).

badger with an average weight of about 15 kg eats daily a quantity

of food equal in all to 3-4% of its live weight.

^{*}Not in Lit. Cit.-Sci. Ed.



842 Fig. 303. Complex old burrow of European badger in mixed fir-larch forest. South of Vyazniki, Vladimir district. October 1964. Photograph by V.G. Heptner.

Home range. Almost no data. The badger, apparently, moves away from its burrow a considerable distance, but is most active within a radius of about 400–500 m from it; i.e., within an area of about 100 h. Isolated ranges, it seems, occur only in those places where badgers are few and the area yields little food. With abundant food, badgers live near each other, sometimes 2–3 families in one burrow of complicated construction. A series of cases exist in which the inhabitants of one burrow visit a neighboring one and peacefully live together (Neal, 1948). In Moldavia, in early spring and late autumn, the radius of badger activity equals 2–3 km; in summer and the beginning of autumn, this range shrinks to 0.5–1.5 km (Korchmar', 1962). In Tataria, in early spring, the badger feeds near the burrow, in summer, it moves away from it for 2–3 km, maximally for 5 (Gorshkov, 1964).

Burrows and shelters. The badger is a typical burrowing animal. Only in very extreme cases, with insufficient places suitable for burrowing, does it creep in winter into a haystack or into a hayloft in a forest glade. In England, there was a case where a badger constructed a surface nest-lair in bushes, where it gave birth to 5 young.



843 Fig. 304. Entrance into permanent burrow of Amur badger, made among stone blocks at the trunk of a Korean pine. "Kedrovaya Pad'" preserve, southern Primor'e.

June 1962. Photograph by A.G. Pankrat'ev.

The number of exits in one burrow fluctuates from 1–2 to 44–50 (Neal, 1948). In the vast old underground constructions of this animal—badger "cities"—several badger families sometimes settle. In this event, most frequently, several systems of passages and nesting chambers occur, most often isolated from one another. Usually, some exits are continuously used, the remaining are only used in case of danger, or serve for the play of young badgers. In Tula abatis (Likhechev, 1956), 68.8% of the breeding burrows had from 2 to 5 exits. Their width at the base is from 22 to 63 cm, height—14–32 cm; they are more often semicircular (arched) form. The nesting chamber is positioned 5–10 meters from the exit opening, at a depth of not less than 1 m from the soil surface, more

often at a depth of about 1.4 m, but in individual cases, it is even deeper—up to 2-3 meters. General length of the passages varies from 35 to 81 m, with cubic capacity of the entire construction ranging from 8.3 to 19.2 m³. In one case, the volume of the freshly thrown-up ground near the burrow was 38 m³ (Moscow dist.). Average dimensions of the nesting chamber are 74×76 cm, with an average height of 38 cm (Likhachev, 1956). Bedding consists of dry leaves and grasses, which are periodically renewed. Leaves are always collected on the dry days. There occur 2-3 nesting chambers. Some of them are open from both ends, and others are blind. In some complicated burrows the system of passages and chambers form certain layers ("floors"). Special "ventilation" passages do not occur in badger burrows. In winter, the openings are closed by ground and leaves. By winter, up to 5 kg leaves and grasses for the bedding are collected and the temperature in this bedding is kept constant. The soil at the depth of the nesting chamber most often does not freeze (Likhachev, 1956).



844 Fig. 305. Occasional day lair of a badger, secluding itself after a night hunt, under a small twisted aspen. Boggy dark aspen wood. In the background of the photo is a small lake. South of Vyaznikov, Vladimir district. October 1964. Photograph by V.G. Heptner.

Spring cleaning of the burrow is connected with birth of the young (Neal, 1948). Each year, apparently, a new nest chamber is dug for the birth. During the course of the summer it is changed, sometimes several times, apparently in order to rid it of ectoparasites. For the same reason, periodic cleaning of the burrow occurs. The main work of building a burrow dates to August–September, when a newly formed pair of young dig a new burrow, and old burrows are prepared for hibernation.

Daily activity and behavior. As a rule, the badger is active at twilight and at night. On bright moonlit nights, activity drops sharply. Time of emergence from the burrow clearly coincides throughout the entire year with the beginning of the twilight (a little after sunset), and changes proportionately with day length (Neal, 1948). Only in extremely remote places does the badger emerge from the burrow during the day, but does not leave it—it usually lies in the entrance and basks in the sun.

Among the sense organs, the best developed of all is smell—it is the main organ of orientation. The badger's vision is monochromatic. The badger does not react to a lantern with red light. Only moving objects attract the badger's attention. Its hearing is no sharper than that of the human. Since it makes significant noise while moving itself, the badger cannot catch the simultaneous movement of a human. In capturing food, it is mainly oriented by smell.

Torpor, winter sleep. Winter sleep in the badger is the adaptation of an omnivorous predator to existence under severe climatic conditions with cold, snowy winter, when its main foods disappear or become unavailable. Winter sleep in the badger, as also in the bear, is not accompanied by a lowering of body temperature and slowing down of all vital functions.

Already in the second half of summer, the badger begins to accumulate fat reserves, which reaches its limit in October. By this time, the burrow is cleaned and the nesting chambers are filled with bedding. In the middle zone of the USSR, the badger retires for winter sleep in the period from the second half of October to the middle of November. It usually stops leaving the burrow after the snow falls. In very warm winters, badger tracks are observed up to the end of January (Tula abatis; Likhachev, 1956). Where winter is not severe and almost without snow, for example in the Trans-Caucasus and England, badgers do not retire at all or its sleep is repeatedly interrupted, especially by thaws.



845 Fig. 306. Hollow next to root of Mongolian oak—temporary shelter of Amur badger during the period of fattening on acorns. "Kedrovaya Pad'" preserve, southern Primor'e. 20 October, 1964. Photograph by A.G. Pankrat'ev.

Upon retiring, the badger blocks the exits of the burrow with dry leaves and earth.

In spring, the badger emerges from the burrow in March-first half of April. In Tula abatis, the average date is 10–15 March, with fluctuation during the multiyear period from 3 to 21–23 March (Likhachev, 1956); in the neighborhood of Gor'ki (A.N. Formozov)—the middle of April. The earliest emergence near Kazan was recorded on 2 April (1955)—the average date—mid-April

(Gorshkov, 1965). It has been noted that the time of the badger's emergence from the burrow coincides with the spring arrival of the white wagtail and the beginning of the nuptial flight of woodcock; however, this coincidence is not always observed. In Middle Russia, the badger usually emerges after this, when the average temperature remains for several days above 0°C. The short warm spells in the beginning of March do not induce emergence of the badger (Likhachev, 1956).

Seasonal migrations and transgressions. Annually, in autumn young badgers disperse. Their dispersal is closely connected with breaking up into pairs and the construction of new burrows. The animals sometimes occupy burrows the inhabitants of which have died. The distance to which young badgers dispense depends upon the food resources of the land. In one case, a pair settled 1.5 km from the parental burrows (Neal, 1948).

Beside such local mixing, cases occur when individual animals appear at a considerable distance from the primary habitat. Thus, in 1951, a badger was found in the upper Pechora, where earlier it was unknown (Teploy, 1960). Such cases are not frequent, but are observed everywhere. How badgers are able to penetrate for such distances during their dispersion and what stimulates them to do this are not known.

Reproduction. Reproduction of the badger is, at the present time, much better studied than in the majority of animals having a latent period of pregnancy. Nevertheless, all data are still contradictory.

In the Moscow zoo, young males copulated at the age of one 846 year, but it is not known whether these matings are productive (Osmolovskaya, 1948). In England, badgers have already united in pairs at the age of one year, but offspring do not occur in the first year, and the first productive mating is observed at the age of 17 months (Neal, 1948). In the G[erman] D[emocratic] R[epublic] and Sweden, adult males are able to fertilize females from January to October, but yearling males, not earlier than in March-April or May (Shtive, 1952*). Testes of these males are found in active condition from mid-March to August (other data from Sweden are contradictory).

Females are capable of reproduction at the age of two years (Osmolovskaya, 1948). On attaining sexual maturity in the second

^{*}Not in Lit. Cit.-Sci. Ed.



846 Fig. 307. Temporary burrow of Amur badger in oak wood on south slope. "Kedrovaya Pad'preserve, southern Primor'e. 20 October, 1964. Photograph by A.G. Pankrat'ev.

year, young females first ovulate either early in spring or in summer and autumn (Neal, 1948). In young strong females, follicles develop during the period of winter repose (in weaker ones—from January to May and later; Unger, 1955). In the middle part of the G[erman] D[emocratic] R[epublic], some of the females born in a given year are fertilized in September–November, and in the particularly warm winters, also in December–January. In Sweden,

the females of that age are not fertilized (Shtive, 1952). Maturation of follicles in the ovaries of English badgers was observed in February–March, as well as mature, recently ovulated follicles. Large, maturing follicles were also noticed in June and September–October (Harrison and Neal, 1956).

Ovulation and formation of new corpora lutea also occur in pregnant females during the whole latent period, but esterus, copulation and fertilization do not take place. Therefore, the number of corpora lutea may be considerably larger than of blastocysts in the horns of the uterus. During the latent period, not less than three ovulations take place. Ovulation proceeds within 72 hours after being provoked by copulation (Notini, 1948). For implantation of blastocyst, there is no need for the stimulation of copulation. The female allows the male access to her only if it has ready mature follicles. In middle Sweden, as shown by materials from several hundred badgers, females are fertilized from May to July. Copulation in July was also observed in Central Europe, and in general here, cases of summer mating are known to be quite numerous (Unger, 1955). In England (Neal, 1948), copulation was observed in March-May, as well as in June-September, and attempts of it are in February, March and the beginning of October. The greatest sexual excitement occurs in February-March. Rut and copulation proceed for short periods, between which the mutual interest in sex disappears. The least sexual activity occurs in May and up to mid-July, when all badger activity is concentrated on food.

In relation to the ability of the lactating females to be fertilized, data are somewhat ambivalent. According to some data (Shtive, 1952)*, they cannot be fertilized during this time, and fertilization occurs in autumn or in the following year. The influence of lactation on the ovulatory cycle has not been shown (Harrison and Neal, 1956). In the Moscow zoo, estrus and copulation in Amur and "sand" (steppe) badgers were observed predominantly in the end of March–April, 3–6 days after parturition, and in individual cases—in July (Osmolovskaya, 1948). Material of 120 badgers from France showed that, in the south of the country, in 80% of the cases copulation takes place during February, just after parturition (Canivenc, 1957).

^{*}Not in Lit. Cit.-Sci. Ed.



847 Fig. 308. Track of a badger, emerging early from hibernation, on deep snow. April. "Stol'by" preserve near Krasnoyarsk. Photograph G.D. Dul'keit.

In badgers, there are two periods of pregnancy: a prolonged period of the latent condition of the fertilized egg, and a much shorter period of active development of the embryos after implantation of the ovum. In the latent period, the fertilized eggs reach the blastocyst stage and are found free in the horns of the uterus. Their nutrition at this time is probably fulfilled by the secretory activity of uterine epithelial cells. In the period March–July, the blastocyst has a diameter from 1.5 to 2.0 mm—this is the primitive trophoblast. From October to December, the blastocyst already has a diameter of 3.5–4.0 mm. Their placentation proceeds in December, when they are evenly distributed along the uterine walls (Canivenc, 1957). In England (Harrison and Neal, 1956), blastocysts were found from 30 April; from placentation to parturition takes 60 days.

In general, the duration of pregnancy the case of summer mating is 271-284 days, and for early spring—up to one year. In

females fertilized in January and later, the latent period extends to the end of December, and the duration of pregnancy consists of 14-15 months (Shtive, 1952)*.

With castration and ovary ligation, it was shown that up to implantation, hormonal secretions of the ovary, including the corpus luteum hormones, have no effect at all on nutrition and development of the blastocysts (Unger, 1957). Introduction of proestrone and progesterone with estradiole did not stimulate placentation. It is possible that the latent stage is the result of the absence of the element necessary for this process, perhaps ovarian hormone. The quick development of the embryos after placentation is coincident with the lengthening of day light; *i.e.* with the effect of cortical hormones (Unger, 1955).

The average number of corpora lutea in material from England (Harrison and Neal, 1956) during the entire period of pregnancy was 6.5 (from 2 to 11), the average number of embryos in January-February—3.1; in Sweden, it is equal to 2.5 (Notini, 1948); in Germany—2.7 (Fisher, 1931).* In England, the average number of young in a litter is 2.25 (1–5); in 22 cases, it was 2; in 8 cases, it was 1 and 3, and in 4 cases—5 (Neal, 1948). In Moscow zoo, the number of newborns ranged from 2 to 5 (average—4). In Kazakhstan, in the Dzhungarsk Alatau, litters were 2–4, in the lower Ili—3–4, and in Tselinograd district—5–6 (Sludskii, 1953).

On the whole, the size of litters varies from 1 to 6 and the number of embryos reaches 7, but most often in the litter 2 badger whelps occur.

In the G[erman] D[emocratic] R[epublic], young are born in March-April; in Sweden—in March; in Western Europe, from 19 December to 14 April. There was one record in July (Neal, 1948). In southern England, [birth] occurs more often in February—March and in the north of the country—more often in March. In the Moscow zoo, in 7 cases parturition occurred in the period 26 March-21 April. Therefore, the reproductive process in badgers is quite complicated. The major periods depend on geographic variations in living conditions. These also have, undoubtedly, significance also for age, and attributes of early or late litter, etc.

In nature, badgers are monogamous, and most often the female copulates with one male; however, rare cases of mating with two

^{*}Not in Lit. Cit.-Sci. Ed.

males have also been observed. The male remains with the female for several years, possibly for its entire life (Neal, 1948).

Growth, development and molt. In England, the newborn badger pups weigh about 85 gm, with body length of 12 cm (Neal, 1948). Weight of newborns in the Moscow zoo was 63-84 gm; on average 75 gm. They are born completely helpless, blind, and with the ears covered by skin. The newborn cubs are covered with sparse. white wool and the dark stripes on the head are well differentiated At the age of 3-5 days, the claws become pigmented and individual dark hairs appear. Strong darkening of color is observed at the age of 10-14 days. The juvenile pelage is replaced at the age of 41-68 days. Ear pinnae are formed at the age of 3 weeks, and eves open on the 35th-42nd day. Milk teeth erupt at the age of 1 month, but are not fully developed, and at the age of 2.5 months, their replacement by the permanent ones begins. Reduction of the milk dentition may be the result of prolonged feeding exclusively on maternal milk. The young shift to independent feeding at the age of 3 months (Osmolovskava, 1948). At the age of 4-6 months, a reduction in intensive growth is observed.

849

At the age of 6–9 weeks, badger pups begin to emerge from the burrow, but they do not decide to abandon it. The first emergence under the mother's protection was noted in England at the end of April. At the age of 11 months, they come out near the burrow to play, but only in the presence of parents. Dispersal of young badgers proceeds in October, and at that time, they break up into pairs.

Enemies, diseases, parasites, mortality, competitors and population dynamics. The badger has almost no enemies. Wolves, lynx, and dogs are dangerous to it, but cases of death from them are very rare. In practice, only human activity has significance for the badger—direct destruction, and also forcing it from occupied areas by destruction of burrows. This latter is particularly severe where possibilities of burrowing are very restricted because of unfavorable ground and hydrological conditions.

In nature, cases are known of a die-off among badgers, after which the animals disappeared from the given locality for a series of years. This points to the effect of an epizootic, but the cause of the die-off were not established. Only an invasion of helminths spreading in badgers is known. The most dangerous of these are pulmonary invasions, in particular eluerostrongylosis and



849 Fig. 309. Track of right paw of badger on moist sand and the scheme of tracks during slow movement of the animal. Naurzum preserve, Kazakhstan. 7 April 1957. Sketch by A.N. Formozov, about 2/3 natural size.

krenozomatosis (Rukhlyadev, 1940). In England, mortality due to acute tonsillitis was recorded (Neal, 1948). The extent of mortality among badgers is unknown. The age limit is supposed to be determined as 12–15 years.

With respect to burrows the badger's competitors are shown to be the red fox and raccoon dog. However, the badger is by no means appears here as the weakest. The old, widespread representation that the fox itself, being not purely carnivorous, drives out badgers from burrows, is untrue. Often, fox and badger live side by side in isolated sections of a wide burrow. However, a series of cases are known where a badger drove away a fox and destroyed its litter, discarding the fox carcasses on the surface (Likhachev, 1956).

In England, badgers often die under the wheels of cars and trains at night, but in the majority of cases, they apparently die in burrows. This is supported by the frequent discovery of skulls and bones in burrow scrapings during cleaning. Apparently, badgers seal the chamber in which the badger died and dig a new one in another part of the burrow. In England, they observed, as a pair of

badgers pulled a badger corpse from a burrow and buried it in a rabbit burrow widened for this (Neal, 1948).

There are fluctuations in badger populations, but have not yet been studied. The greatest influences on them are rendered by humans and diseases. In England, for example, a considerable increase in their number was recorded in the war years in connection with the cessation of its pursuit by humans (Neal, 1948).

Field characteristics. In twilight and night time, the badger can be detected in the forest by its noise made while moving and feeding. Under the cover of darkness in distinction from the masso jority of wild animals, it does not conceal itself, and is heard from a far. Characteristic signs indicating the presence of the badger are the beaten tracks going in various directions from its burrow to a distance of up to 0.5 km, numerous, very typical holes made by it while catching mouse-like rodents, beetles and their larvae, destruction of bumble bees and wasps nests, and also by overturned forest litter, and feces left here and there.

Tracks of badger on dirt, moist soil or on sand are difficult to confuse with anything else. They resemble most of all tracks of bear in miniature. Prints of the plantigrade feet and long, massive claws are particularly characteristic of them. Most often, prints of the tracks occur in pairs—prints of hind and fore paws overlap each other. Length of the forefoot is about 8 cm and of hind—about 9 cm; length of claws of fore paw in prints is about 2.5 cm, length of doubled prints of the track, about 10–14 cm (Formozov, 1957).

Practical Significance

In the hunting economy, the badger has little, mostly local, significance. The price of fur product from it is not high. The skin is used for shagreen [leather] and the guard hairs for making shaving brushes of high quality. Badger meat is eaten in several districts; however, in the majority of cases, it is thrown away. Badger fat is highly valued, in Middle Russian districts (Moscow, Vladimir) for example, and the badger is mainly hunted for its fat rather than its less valuable skin. The fat is used for greasing leather, but it is chiefly used in folk medicine in case of injuries, rheumatic diseases and even tuberculosis; *i.e.*, analogous to bear fat. On the market, it is very scarce (V.G. Heptner).

Not less than 50% of the yearly catch of skins is obtained from Kazakhstan and other Middle Asian republics of the Union. Here the badger constitutes about 5% of the commercial fur trade and in other places considerably less.

At the same time, the badger is useful in destroying insects and mouse-like rodents harmful to forestry and agriculture. Among insects and their larvae that are destroyed in great numbers are—larvae and adults of maybeetles, larvae of mountain leafhoppers, mole crickets, locusts, larvae of longhorn beetles and sawflies. Among mouse-like rodents, the common vole has greatest significance in its food, and pests of forestry and agriculture. The badger feeds also on injured animals and birds, and on their carcasses. Harm caused by the badger to the hunting economy is very insignificant. The accusation of badger attacks on small domestic livestock is not confirmed. In England such cases in relation to domestic fowl were observed, but very rarely.

Methods of hunting the badger vary, except that the badger does not serve as the object of special hunting. Badgers are caught in jaw traps, or opportunistically by night hunting with dogs, ambushed at burrows with guns, and also caught with special dogs (fox-terriers and dachshunds) used to excavate the burrow. Finally, the badgers are sometimes smoked out of their burrows, but more often, they die in the burrow.

Calculated against the useful activities of the badger, its taking in the zone of broad-leaf forests and forest-steppe and in the regions of field-protecting forest belts should be entirely prohibited throughout the whole year, as also should, any kind of excavation and damaging its burrows, especially where the number of badgers is determined by the conditions for burrowing. Spring and summer hunting should be prohibited everywhere as well, except in the autumn months: from 15 August or 1 September to 1 November (P.Yu.).

Subfamily of Otters

Subfamilia Lutrinae Baird, 1857

Genus of Otters

Genus Lutra Brisson, 1762

1762. Lutra. Brisson. Regn. Anim., 13. Mustela lutra Linnaeus.

Dimensions large.

General construction light, body strongly elongated and thin, extremely flexible; head small, small ear pinnae; tail long, extremities strongly shortened, plantigrade, claws small, between fingers webbing strongly developed. Pelage very close-fitting, with coarse guard hairs and very dense, soft underfur. Color almost constant over whole body, more or less lightening on lower surface, of tawny tone. Glandular area at base of tail absent. Teats 2 or 3 pairs.

Skull relatively light, broad and strongly flattened, with strongly diverging zygomatic arches and very sharply narrowed postorbital region. Braincase volume enlarged, rostral region short and broad—its width greater than length. Posterior part of hard palate lying posterior to toothrow narrow and relatively short. Mastoid processes flattened, approaching anteroventral part of occipital crest, paroccipital processes low but separated from auditory bulla. Mastoid width of skull a little less than zygomatic. Auditory bullae flattened, with small bony auditory meatus.

Dental formula $I \frac{3}{3} C \frac{1}{1} P \frac{4}{3} M \frac{1}{2} = 36$. In its main features, the

dentition is like that of the badger subfamily, Melinae. It also represents the same combination of cutting and tubercular (grinding, crushing) type, with however, great development of incisor characters. Compared to the general dimensions of the rostral part of the skull and of the palate, the dentition is large. Upper carnassial tooth large and triangular in form. Upper molar rhomboidal in form, its area approximately equal to carnassial or very slightly less. Lower carnassial tooth long, anterior part has three well-developed apices; posterior part a little longer than anterior. Loss of anterior premolars usually does not occur.

Specialized freshwater forms, excellent swimmers and divers. always connected biotypically with water bodies, both in plains and in part, mountains. Swims both by paddling movement of the limbs and by sinuous bending of extremely flexible trunk and tail. Feeds mainly on fish, in part on aquatic invertebrate (crayfish) and amphibians. Builds bank burrows. Hibernation is absent, apparently, as is a latent stage in development of the fertilized egg.

The range of the genus is extremely extensive—one of the very largest among mammals. It is exceeded only by the ranges of several bats. This is particularly remarkable, given the great specialization of species in the genus and the relatively small number of them (see below). The genus is distributed throughout Europe. occupies the mainland of Asia (except the extreme north and Arabian Peninsula), Ceylon, Sakhalin, the Japanese islands, Taiwan, Hainan, Java, Sumatra, Calimantan (Borneo) and Banka. Representatives of the genus are absent on the remaining islands of the Pacific Ocean1.

In Africa, the range includes the extreme northwest of the 853 continent (Atlas countries) and the entire continent south of the Sahara, except its extreme southern and southwestern parts. In North America, the range occupies the whole continent, except several areas in the extreme north and desert regions in the south, the islands adjacent to the continent along its western shore (Kodiak, Alexander archipelago; absent on islands of the Bering sea), and islands off the northeastern shore (Newfoundland and some smaller ones). In the range is included Central America and South America, and the whole of Tierra del Fuego. In the range is included the island of Trinidad, but species of this genus are absent on all islands of the West Indies. The range of the genus, therefore, occupies almost the entire range of the subfamily—its species are absent only on Palawan, Commander, Aleutian and Pribiloff islands, in middle India and in South Africa, where species of other genera are encountered.

The genus Lutra is the very largest in the subfamily. In it are 11 species of the 16 assigned to Lutrinae. There were attempts to divide it into several independent genera (Lutrogale for

^{&#}x27;Information on the Kuril islands is incorrect (see below, in description of 851 otter). Pocock's reference to its occurrence in the Philippine Islands is, apparently, wrong-it was not confirmed by anyone. In the Philippine sensu stricto, true otters are absent, but the clawless otter, Aonyx cinerea, exists on Palawan.

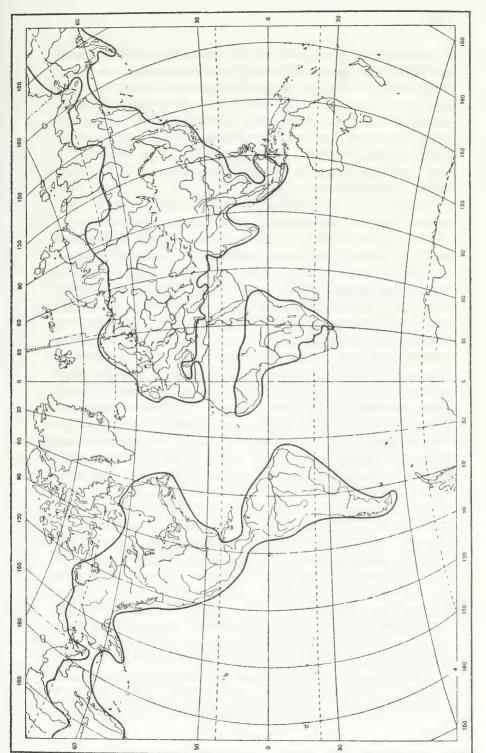


Fig. 310. Range of the genus of true otters, Lutra Briss. V.G. Heptner.

L. perspicillata, or Hydrictis for L. maculicollis); however, the majority of authors do not accept this division, and it is, apparently, more correct to recognize one genus with two subgenera—Lutra and Lutrogale. On the other hand, some authors (Chasen, 1940; Carter, Hill and Tate, 1946) believe that the separation of the genera (subgenera) of the so-called clawless otters Aonyx (capensis) and Amblonyx (= Microaonyx: cinerea) has no basis. They combine the species mentioned with Lutra, which is an hypothesis that demands a wider foundation.

Besides the most widely distributed Palearctic and Indo-Malayan species, the common otter, L. lutra, the genus also includes the following species: L.* canadensis (North America, southward to Mexico)2; L. sumatrana (Indo-China and Malayan archipelago; evidently, the least specialized species); L. maculicollis (Africa south of the Sahara); L.* annectens (extreme south of North [America]. Central and South America): L.* enudris (South America); L.* felina (southern South America; a marine form, evidently the most specialized form in the genus); L.* incarum (South America); L.* platensis and L.* provocax (the same; subgenus Lutra) and L. perspicillata (South and Southeast Asia; subgenus Lutrogale). Therefore, the greatest richness and diversity of species are obviously, characteristic of South America (the center of origin)—there are 6 species out of 11 here. North America is characterized by 1 species, there are 2 species in South Asia (one represents a separate subgenus), 1 species in Africa and 1 species has the above-mentioned wide distribution in Eurasia and northwestern Africa. It is noteworthy that with the great diversity of otters in South America (besides those mentioned, there is also the giant river otter. Pteronura brasiliensis). North America possesses only one endemic species. One is characteristic also for northern Eurasia—apparently the diversity of forms in the genus is in the south. In this sense, geographic variation of L. lutra is also indicative (see below).

As already mentioned (see characters of the family), in this complicated mix of forms representing the marten family,

^{*}These New World species, here placed in *Lutra*, are now considered a distinct genus, *Lontra*—Sci. Ed.

²This form, with its great general similarity to the Eurasian otter, itself represents a separate species, well characterized craniologically. The separate species, *L. mitra* (Prince Wales Island in Alexander archipelago), accepted by American authors, represents only a subspecies of *L. canadensis*.

Mustelidae (perhaps itself a polyphyletic group), the subfamily of the otters—Lutrinae—is one of the most accurately circumscribed. Perhaps it may even be considered the most natural and sharply distinguished one.

Besides the genus *Latra*, the subfamily includes 4 other genera, the so-called giant river otters: *Pteronura*, in South America (1 species—*P. brasiliensis*), the clawless otters, *Aonyx*—a genus comprising two species belonging to two subgenera—*A.* (*Aonyx*) capensis in Africa and *A.* (*Amblonyx*) cinerea in Southeast Asia, *Paraonyx*—with 1 species in West and Central Africa (*P. congica*: "species" *microdon* and *philippsi* are not taken into consideration here) and sea otter* (*kalan*)—*Enhydra*, with 1 species (*E. lutris*) from the shores of the northern part of the Pacific Ocean (see below).

The identification of the position of *Lutra* within this circle of genera is very difficult. The thing is that within the limits of the subfamily, the genus of sea otters ("kalan")—Enhydra—is totally sharply set apart from all the genera of the subfamily by the extremely unique structure of its limbs, skull, completely distinctive teeth and other characters (see description of this form below). All the remaining genera (and species), together and separately, are very far different from Enhydra and are, to a greater or lesser degree, close to each other. Differences between them are completely unequal to differences between each of them and Enhydra. By this criterion, they might perhaps be considered as one genus; so to speak, river otters, *Lutra*; corresponding to the genus of sea otters, Enhydra.

Characters of external structure and craniology, by which the otters are usually grouped, create patchwork combinations. Thus, the group Aonyx has no claws (A. capensis) or they are very small (A. cinerea). This [latter] is usually considered a specialized character ("progressive"). At the same time, finger webbing is reduced or actually almost absent as in the posterior limbs of A. capensis. Their skulls are relatively short with a voluminous braincase. The dentition is modified only weakly and unsubstantially. As regards the structure of its skull, extremely developed, large finger webbing and certain other characteristics, evidently the entire genus Lutra must be considered a highly specialized ("progressive") group

^{*}In Russian original, "Kamchatka beaver"-Sci. Ed.

among the genera of freshwater otters. Most closely related to it, apparently, is the genus of giant Brazilian otters *Pteronura*. The southern Asiatic and African *Aonyx* and *Paraonyx* are, apparently, more primitive, although *Aonyx* is also very close to *Lutra*.

In its origin, the subfamily is apparently connected to certain extent with the subfamily of badgers, Melinae. However, the earliest representatives of the subfamily as highly specialized forms are already known from the Upper Oligocene of Europe (Potamotherium). More than 10 genera of fossil otters have been described, mainly from the Upper Tertiary period (Miocene, Pliocene—Paralutra, Enhydriodon, Vishnuonyx, Sivaonyx and others) and partly from the Pleistocene (Cyrnaonyx). The genus Lutra is known from the Lower Pliocene of Europe and Asia and from the Upper Pliocene of America.

All the species of the family, even in the tropics, represent valuable fur animals.

In the USSR, there is one species: Lutra (Lutra) lutra Linnaeus, 1758, which represents about 0.3% of the species of the fauna and about 10% of the species in the genus.

The range occupies almost the whole territory of the country. The species is everywhere closely associated with water.

A valuable fur-bearing animal (V.H.).

Subgenus of the Common Otters

Subgenus Lutra Brisson, 1762

[EURASIAN] OTTER, PORESHNYA

Lutra (Lutra) Linnaeus, 1758

- 1758. Mustela lutra. Linnaeus. Systema Naturae, ed. X, 1, p. 45. Uppsala, Sweden.
- 1777. Lutra vulgaris. Erxleben. Regn. Anim., 1, p. 448. Renaming of lutra.
- 1834. Lutra nudipes. Melchior. Den Danske Stats og Norges Pattedyr, p. 50. Coast of northern Norway.
- 855 1839. Lutra aurobrunnea. Hodgson. J. As. Soc. Bengal, 8, p. 320. Nepal.

- 1839. Lutra monticola. Hodgson. Journ. As. Soc. Bengal, 8, p. 320. Nepal.
- 1844. Lutra kutab. Schinz. Syn. Mamm., p. 354. Kashmir.
- 1867. Lutronectes whiteleyi. Gray. Proc. Zool. Soc. London, p. 181. Japan.
- 1912. Lutra lutra seistanica Birula. Ezhegodn. Zool. mazeya Ak. nauk, 17, p. 274. Gil'mend river in Seistan, eastern Iran.
- 1915. Lutra lutra oxiana. Birula. Ezhegodn. Zool. muzeya Ak. nauk, 19, p. XXI. Lyangar, Pyandzh basin. Western Pamir.
- 1922. Lutra vulgaris var. baicalensis. Dubowski. Arch. Tow. Nauk. Lwow, 1, p. 349. Nom. nud. Near Baikal.
- 1922. Lutra vulgaris var. amurensis Dybowski. Ibidem, p. 349. Nom. nud. Amur and Ussuri Territories.
- 1922. Lutra vulgaris var. kamtschatica. Dybowski. Ibidem, p. 349. Nom. nud. Kamchatka.
- 1931. Lutra lutra meridionalis. Ognev. Zveri Vost. Evropy i Sev. Azii, 2, p. 527. Vic. of Teheran, Iran.
- 1936. Lutra stejnegeri. Goldman. Journ. Mammal., 17, p. 164. Vic. of Petropavlovsk, Kamchatka (V.H.).

Diagnosis

The only species of the genus in the USSR.

Description

Body strongly elongated and relatively thin, more or less equally thick along its whole length—posterior part only slightly more massive than shoulder region. Limbs short, from whence its stature. Tail long and comprises about half the length of head and body, very thick at base, strongly narrowing to tip and flattened in dorso-ventral direction. Such tail structure is determined by strong development of ligaments but most of all by the powerfully muscular tail tracts running along the vertebrae. Moreover, masses of collagenous tissue are strongly developed along the lateral sides of the tail, somewhat less on the lower side, and still less on the upper side, forming loci for fat deposition. Tail thickness, therefore, depends to a certain degree on nutrition of the animal, and characterizes it. The tail, contrary to all remaining species of the

family (except sea otter, does not bear long hairs. It is covered by short (as on the trunk or shorter) closely investing fur.

Head relatively small, elongated oval, narrow, no wider or hardly wider than the neck, strongly flattened. Neck relatively short. Ears short, with rounded apexes, weakly protruding from fur, widely separated. External ear openings covered by special valves. Eyes quite large; bare area on tip of nose large, transversely elongated—its width greater than its height or approximately equals to it. On the whole, the appearance of the otter's head is somewhat snake-like.

Digits fused together by strongly developed webs, reaching middle or nearly to end of distal phalanx. Digits, including first, somewhat elongated, which increases area of hand and foot. Second and third digits on both fore and hind limbs are longest, and equal in length. Lower hand and foot naked, edged with elastic hairs somewhat increasing propulsion surface. Claws small, but relatively little reduced.

The otter body is extremely flexible and the animal is very active. On land, the otter moves in a walk or trot, with lowered head, bent back, and outstretched tail usually dragging its end on the ground; more rarely leaps, strongly hunching [its back]. On the whole, its movement on land is not very agile. Movements of otter in water are particularly confident and agile. Swimming slowly, it usually paddles with its paws but when moving quickly, it presses limbs against body and moves with energetic snake-like movements of the whole trunk and muscular tail. The moveability and flexibility of the vertebrae and entire body of the animal are exceptional. Overall, in general appearance and habits, the otter is entirely unique and is strongly differentiated from all remaining species of the families of our fauna.

Pelage in winter is short, very even over the whole body (difference between length of hair on back and belly is small), close-fitting, shiny, with often coarse, elastic guard and very dense and close-fitting soft, silky underfur. The fur on the belly is denser than on the back. In northern otters, the average length of contour hairs on the back averages 24.2 mm, on belly 21.0 mm; guard hairs, correspondingly, are 18.4 and 17.2 mm, and underfur 14.6 and 11.2 mm. The number of hair on 1 cm² of dorsum reaches 35,000 (34972), on venter about 50,000 (50668). On the back, for every outer hair, an average of 155 underhairs occur and on the



Fig. 311. Otter, Lutra lutra L. Sketch by A.N. Komarov.

belly—120. Outer hairs have very wide and flattened distal thirds the ratio of their width to length is 1:3-3.5 (in terrestrial forms, not more than 1:1.5-2.5). Moreover, the outer hairs are strongly inclined with respect to the skin surface (30-35°) and are strongly bent near the base ("in the neck") where they are relatively thin. On the whole, the outer hair has the form of a small plate and together they tightly cover over the underhairs. The bases of these latter, as well as bases of the smallest top hairs, are strongly crimped and form a wavy fur coat. All these characters, especially the structure of the outer hairs, themselves represent typical adaptations to an aquatic mode of life, and they prevent wetting of the fur, even during extended immersion in water. The cortical layer of the hair 857

is greatly increased, thus its durability greatly augmented (Tserevitimov, 1958)³.

Full growth of the otter is attained only in the third year of life; at that time, its fur is also completely developed. Skins of animals born in the current year ("koshlak") have a long and soft pelage composed of sparse underfur and thin, soft guard hairs. In second-summer animals, the fur is longer and softer than in adults, but coarser than those born in the current year, with sparse underfur.

Glandular areas at the tail base are absent; anal glands are present, but not strongly developed (?). Teats 2-3 pairs⁴.

Color of the upper body in winter fur is bright dark-brown or dark nut-brown. Upper head somewhat darker, tail of the same color as back. Lower surface of body, including ventral neck and lower and lateral head are slightly lighter, with tinge of silvery yellowish tones, sometimes whitish. On the sides, the color forms a gradual transition from the tone of the back to the color of the belly. Legs are dark brown, and claws light horn, darker at the base.

In summer coat, the fur is somewhat more sparse, but of the same color as in winter. There are no differences among sexes in color. Individual variability of fur is insignificant and lies only in more or less intensity, and in greater or lesser lightening of venter relative to dorsum. In some localities, two color types are differentiated—lighter and darker (G.F. Bromlei; southern Ussuri Territory); however, color dimorphism does not occur. This is normal, simple individual deviation, apparently, even mostly age variation.

The soft "fluffy" fur of the young otter is dark-chocolate color and lacks luster. At first winter, the young animals don a coat similar in color to that of the adult, but their venter is darker than in adults. Upon attaining the adult condition, color continues to change somewhat, and later color changes in the direction of

³Otter fur is considered very durable and "long-wearing" and in determining the relative quality of other furs, its "long-wearing" is accepted as 100. In mink, it equals 70, in sable 50 and in squirrel 25 etc.

⁴For otters of England, 3 pairs recorded (inguinal; Miller, 1912), for middle European 2-3 pairs (Gaffrey, 1961), for our otters, 2 pairs (Ognev, 1931), for the Indian form of the species, 2 pairs (Pocock, 1941).

⁵It is considered that the dark otters, called "river", have a uniform dark-brown color and small dimensions, and live in rivers. The other form—"sea" otter—is larger, its color is lighter—with a dirty-ocherous belly and legs, lives and feeds in the sea (G.F. Bromlei). Similarly, two types of color were also noted for otters in the upper Amu-Darya basin (Chernyshev, 1958).

lightening of the general fur tone, while the venter becomes lighter relative to the dorsum.

Geographic variations of color within the USSR are insignificant and are only expressed in lightening of the general color tone, relatively greater lightening of venter, and decrease in the fur density in some southern regions.

The skull is very broad, both in rostral, and particularly in the zygomatic and cranial regions, and is strongly flattened. Height of the braincase in its middle section constitutes only slightly more than half the mastoid width. Height in the region of the auditory bullae is less than mastoid width. The upper line of the skull profile is almost straight—it is only insignificantly depressed in front of the middle of the interorbital area; and in the young—also in the occipital region. On the whole, this line is almost parallel to the line of the lower surface of the skull. Such a flattened skull is absent in any other carnivore of our country.

The braincase is very voluminous and broad in its middle and posterior parts. The width of this region is increased still more by strong development of the occipital crest which extends also onto the lateral surface of the skull, and the mastoid processes, which are strongly flattened and fused with them in its anterior part. The anterior region of the braincase (in the interzygomatic area) is sharply narrowed. The postorbital area is sharply narrower and forms a strong intersection, particularly striking to the eye thanks to the wide separation of the zygomatic arches. Width of the postorbital constriction is considerably less than the width of the interorbital area and is approximately 4 times less than mastoid width. Postorbital processes are well developed, but short and blunt, and border only a very small part of the orbit.

Orbit quite large—its greatest diameter almost equal to interorbital width. Zygomatic arches are strongly separated laterally throughout their whole extent (as well as in anterior part) and generally form a rounded figure. They are strong and massive, noticeably curved upwards, and in the anterior part bear a well defined tubercle on their upper edge, bordering the orbit from behind and below. Infraorbital foramena, perforating base of zygomatic arch anteriorly, very large. Its diameter is 1.5–2 times more than diameter of the cusp of the upper canine.

Rostral part of skull very short (about 2 times shorter than cranial), high and broad. Distance from anterior point of zygomatic

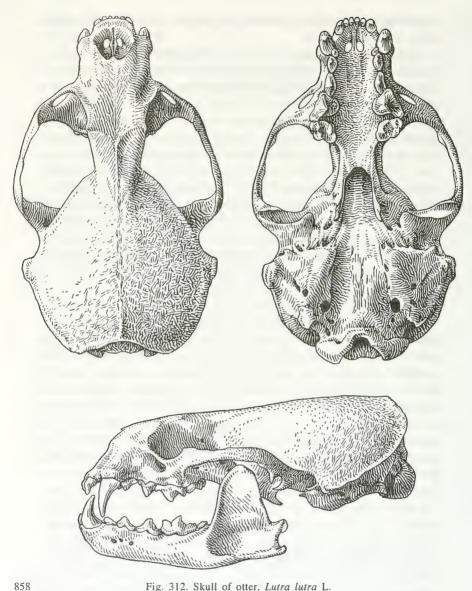
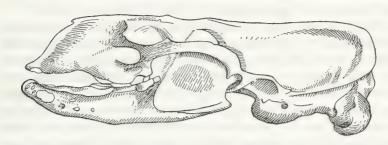


Fig. 312. Skull of otter, Lutra lutra L.

arch to anterior edge of alveoli of incisors approximately equal to width of muzzle below canines, and approximately 4.5 times less than condylobasal length of the skull. Sagittal crest is almost undefined or only weakly so. Palate between toothrows relatively quite narrow and elongated—distance between inner parts of



859 Fig. 313. Skull of a very old otter, Lutra lutra L. Posterior cheek teeth only remain, worn to gums. Sudzukhinsk preserve, southern Primorye. Sketch by G.F. Bromlei.

molars fits into length of palate from anterior edges of alveoli of incisors to posterior edge of molars about three times. Portion of palate lying behind the toothrow is wide anteriorly, quickly narrows posteriorly, and is short. Its length is approximately equal to distance between canines. Interpterygoid notch narrower anteriorly than posteriorly.

Auditory bullae small, flattened and only insignificantly swollen along inner part. Paroccipital processes have form of short rounded outgrowths and do not contact auditory bullae. The external auditory meatus is short, opens below mastoid (anterior) part of occipital crest, and are directed forward and upward. The lower jaw massive compared to general lightness of skull. Coronoid part short, but quite wide, its apex not pointed.

Compared to general dimensions and width of palate and rostrum, teeth are large—maximum transverse diameter of upper carnassial tooth constitutes half of distance between carnassial teeth. Canines are thin, long and very sharp. All small premolars are well developed and of tearing form, and by their location in relation to teeth of opposite jaw (upper—lower), form a strong tearing apparatus. First upper premolar well-developed and not reduced. It is displaced deep into the toothrow and does not lie directly behind the canine, but on its intero-posterior side.

Upper carnassial tooth large, quite regularly triangular in form, one angle directed inward. It bears a high cutting apex along outer edge, behind which lies a second apex, shorter and connected with first by a crest. In front of the main apex lie small teeth. All of them are arranged regularly next to one another. The inner blade,

the area of which constitutes about half the area of the tooth, is flat and does not bear apexes.

Upper molar large, rhomboidal in form. Its area is approximately equal to area of carnassial tooth or slight smaller, and its greatest diameter is directed almost at a right angle towards the axis of the toothrow. The flat surface of the tooth bears four small tubercles, of which two are along the outer edge. Lower carnassial tooth elongated in form, with three well-developed sharp apices, almost identical in dimensions on the anterior part of the tooth. Posterior half of tooth somewhat larger than anterior one and does not bear sharp apices. In area, second lower molar significantly smaller—approximately three times—than carnassial.

Sexual dimorphism of the skull is well manifested. Beside somewhat smaller general size, the female skull is distinguished by almost complete absence of a sagittal crest, even in old individuals, somewhat smaller infraorbital foramen, narrower rostral part of skull (breadth above canines), somewhat smaller nasal opening, and, apparently, somewhat narrower and shorter interpterygoid notch. Skulls of young animals have less-developed protuberances, crests, etc., and are less angular; nasal region is relatively low, lower than occipital region (with age, massiveness and height of anterior part of skull increases), postorbital region is broader and the supraorbital processes are small (Ognev, 1931). Sagittal crest does not develop and occipital is very small. Geographic variation of the skull within the USSR was not noted, and if expressed, then very weakly.

Posterior section of os penis is thickened and somewhat elevated. On anterior end has two rounded lobes, tips directed downward separated by groove. Left lobe 1.5 times thicker than right and ventrally bears incision (Ognev, 1931).

Ratio of body length to length of intestine (two males) 1:6.36 and 1:6.10; cardiac index (male, January) 13.8 (from data of Chernyshev, 1958; Pyandzh basin).

Body length is 550-950 mm, length of tail 260-550 mm, hind foot length 110-200 mm, ear length 17-25 mm.

Condylobasal length of male skull is 107.0–126.0 mm, of females 96.5–121.0 mm; zygomatic width of males is 62.0–83.0 mm, of females 60.5–72.0 mm; interorbital width of males is 17.5–22.5 mm, of females 16.2–21.3 mm; postorbital width of males is 12.3–18.3 mm, of females 11.8–18.3 mm; mastoid width of males is 54.5–71.3 mm, of females 55.9–67 mm.

Weight of adults 5.7-10 kg.6

Females, as is evident from the craniological indices presented, are noticeably smaller than males. Differences in body dimensions and weight of individuals from one restricted territory (Sudzukhinsk preserve in southern Ussuri Territory) are as follows (15 specimens): body length of males; 550–810 mm, of females 550–680 mm; tail length of males; 280–455 mm, of females 280–380 mm; hind foot length of males, 110–120 mm, of females 82–93 mm; ear length of males, 19–25 mm, of females 17–22 mm. Maximum weight of males is 9470 gm, of females, 6543 gm. Animal in the first year of life, in November–February, have a body length of about 350 mm and weight from 1100–1500 gm (G.F. Bromlei).

861 The latter figures are relatively small—young otters from Pechora (preserve; Z[oological] M[useum of] M[oscow] U[niversity]) in November–February weighed 2250, 2400 and 4430 gm (males) and 2250 and 3500 gm (females).

Very old individuals approaching the age-limit experience poorer nutrition than those of intermediate age and, despite sometimes large dimensions, weigh less (G.F. Bromlei). Nutrition and weight change seasonally.

Length of os penis is 58-65 mm.

Geographic variation of dimensions within the boundaries of the USSR was not noted, but some, apparently, exists, and southern otters are somewhat smaller than northern. Several forms from the extreme south of Asia (nair, barang) are quite strongly differentiated by their dimensions (V.H.).

Geographic Distribution

In Europe, Asia except the extreme north and Arabian Peninsula, and in northwestern Africa.

⁶Data on body dimensions and weight from Ognev, 1931; Novikov, 1956; Stroganov, 1962; G.F. Bromlei and from materials of the Z[oological] M[useum of] M[oscow] U[niversity]. Skull dimensions from Ognev, 1931; Stroganov, 1962 and collections of Z[oological] M[useum of] M[oscow] U[niversity]. Altogether approximately 150 skulls. Reference to body length of 100 cm and weight of 15 (16) kg (Central Europe; Gaffrey, 1961 and several other sources) is apparently an exaggeration. In any event, such measurements and weight were not recorded in our otters, even the very largest populations. However, one case is known of an otter caught in Turkhan Territory with tail length (measured from skin) of 175 cm (Zalesskii, 1930). It is possible that this is a case of gigantism, analogous to kolonok and polecat (see [above]).

Geographic Range in the Soviet Union

Very vast and constitutes the greater part of the range of the species. It occupies almost the entire territory of the state except the extreme north and arid and desert regions.

In the European part of the USSR, the northern border of the range on the west is formed by the northern coast of the Kola Peninsula (also exists on Kil'din [Island]) and eastward along the White Sea coast as far as the mouths of the Kuloi and Mezen' [rivers]. On the Kanin, the otter as a permanent inhabitant is absent, but it is sometimes transient there. Eastwards to the Pechora delta, the border passes along the seashore, but beyond the Pechora, somewhat lowers and turns to the south, and reaches the Urals somewhat farther from the sea. However, here also there are places of transgression into the tundra (Malozemel'sk and Bol'shezemel'sk; V.Ya. Parovshchikov). In the Urals, the border falls approximately along the Arctic circle (Shvarts, Pavlinin and Danilov, 1951).

In the northwest of western Siberia, the border passes somewhat to the north of Salekhard and along the extreme southern edge of Yamal (upper Yana river). Going to the east, it crosses Ob' gulf at its southernmost part and passes to the eastern shore of the Ob' gulf at the Arctic circle (Laptev, 1958). Farther, at the same latitude, it crosses the lower Pur and passes beyond the Taz approximately 100 km north of Sidorovsk on the Arctic circle and at the same level or a bit south of the upper Turkhan. Thence, the border suddenly rises to the north, crosses the Yenisei, and east of the Yenisei, Lomo Lake (at Norilsk) and on to the southern Taimyr, reaching there the upper Avam (right tributary of upper Pyasina) at a point a little north of 70° N. lat. It also includes the Kheta (V.N. Skalon), apparently, in its upper and middle course. The Avam is the most northernmost point of the range in the USSR. The otter is absent along the lower Khatanga (Middendorf, 1867).

There is a reference to otter hunting in West Siberia, on the Gydansk Peninsula in the upper Yuribei about 71° N. lat., in the northern part of the tundra zone (Laptev, 1958; Stroganov, 1962). This information is very doubtful, and if it is true, speaks only to occasional long transgressions.

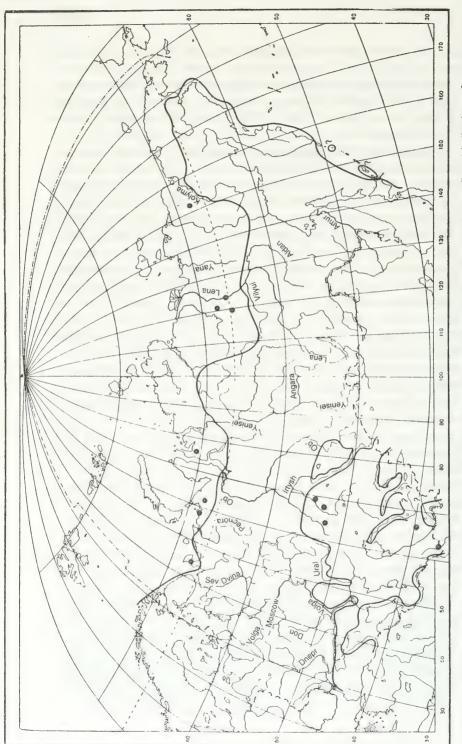
The eastern border is very poorly known; however, it can be considered established that in Yakutiya (especially in the west and

middle) bends considerably towards the south and then again rises strongly to the north in northeastern Siberia. This is, apparently, connected with particularly low winter temperatures in this part of Siberia, leading to formation of very robust ice cover, to freezing of many water bodies to the bottom and even to freezing of small montane creeks.

The course of the border in the eastern half of Siberia is drawn in the following form: from southern Taimyr, the border in a way not yet completely established, goes to the southeast to the upper Vilyui in the region of Chona mouth (about 62°45' [N. lat.]. Then, directing itself towards the east, it crosses the Ygyatta (Igetta) 863 river and several other left tributaries of the Vilyui (Tyung, Tyukan) and passes to the lower Vilyui below Vilyuisk. Thence, the border passes generally in the same direction, crosses the Lena somewhat below the mouth of the Vilyui, extends through the middle courses of the right tributaries of the Aldan—the Tumara and Tompo and passes to the sources of the Indigirka and upper Oimyakon. Then, it goes along the left tributary of the Kolyma—the Yasachnaya river, approximately at Sredne-Kolymsk and to the right tributaries of the Kolyma-the Berezovka and Omolon (border in Yakut according to data of Maak, 1859; Tugarinov, Smirnov and Ivanov, 1934; Belyk, 1953 and Ognev, 1926, and mainly from material made available by D. Ivanov, Yakutsk).

Along the described northern border (not considering the Omolon), the otter is very rare and only individual cases where the animal or its tracks are encountered are known. The border of normal, regular occurrence lies to the south. Nevertheless, there are some less definitive data (Maak, 1859) on occurrence (very rare) of otter along the left tributary of the Lena—the Muna—which flows into the Lena from the left at 68° N. lat. and, a little to the south—on the "Serka" river (apparently the Syarga) in the upper Linda (approximately on the Arctic circle west of the Lena) and at Zhigansk on the Lena—a bit north of the Arctic circle.

These data are in poor agreement with contemporary materials and invite doubt. It is possible that they refer to occasional individuals transgressing far along the Lena. Mentions of "Alazeya in Middle Koymsk region" (Belyk, 1953) obviously belongs in this category. The same may be said of the upper Alazeya (Stroganov, 1962, plotted this occurrence on the map very far to the north).



862 Fig. 314. Range of the otter, Lutra lutra L., in the USSR. Outlined islands of the Kuril chain are old, unconfirmed indications of occurrence the place of probable union of northern and Caucasian parts of the range. Points outside border of range designate the places of transgression Kharimkotan (north), Iturup and Kunashir. Question marks in Tyan'-Shan' and Altai are assumed occurrences; also along the Azov [Sea] coast of individual animals. The most northern occurrence is Yuribei in Yamal. V.G. Heptner.

In the lower Kolyma and along the Bol'shoi and Malyi Anyui it is, apparently, absent. Farther to the east, the border includes on the north the Anadyr basin, and the range also includes its left tributaries—Belaya, Tanyurer and Konchalan (Belopol'skii, 1937; Portenko, 1941). At the mouth of the Anadyr', the border passes to the Pacific Ocean.

The range includes Sakhalin and Shantar Islands (at least Bol'shoi Shantar; Ognev, 1929). There are no data concerning Karagin Island. Of the Kurils, the otter was recorded for Kharimkotan (Kharumukotan) in the north and Iturup (Etorofu) and Kunashir' (Kunasir') in the south (Sergeev, 1947).

On the whole, data on occurrence of otter in the Kuril chain are confused and contradictory. Several authors, both geographers (Solov'ev, 1946) and zoologists (Kuznetsov, 1949) do not refer to this species at all in the composition of the fauna, and according to new data (V.G. Voronov) it is actually absent there. The reason for mention of the otter was probably its confusion with the Kamchatka beaver (sea otter—*Enhydra lutris*) and old information of Snou (1902) who recorded for Iturup and Kunashir the "abundance" there of "river beaver, *Lutronectes whiteleyi*"*.

The southern border of the otter's range in the European part of the country, starting from the mouth of the Danube, generally passes along the Black Sea coast to the mouth of the Dnepr, and farther, around the extreme south of the steppe to the mouth of the Don. In the Crimea, the otter is absent. In the past the otter lived, apparently, in small creeks in the southern steppes. Farther, the border of the range extends along the Don and somewhere in the region where the Don and Volga come close, passes to the Volga. Along it, the otter spreads to the very delta.

To the south of the Don and Volga, in the Trans-Don, Kalmytsk and a considerable part of the Cis-Caucasian steppes the otter is absent. It is encountered along the Kuban', Kuma and Terek (no data concerning Manych), and the line extending along the Kuban' and Kuma represents the northern border of the Caucasian part of the range. To the south of it, the otter exists throughout the entire Caucasus. The Caucasian part of the range, therefore, is isolated from the northern. The possibility, and even the probability, exists that, in the past, the otter lived along the rivers flowing into the

^{*}This "species" is a synonym of L. lutra—Sci. Ed.

Azov Sea between the Don and Kuban', and thus isolation by the steppes was not so complete. It may also be assumed that, under certain conditions, contact between populations might have occurred between the Kuma and Volga.

The otter is absent in the steppes between the lower Volga and Ural [rivers] and in Saratov Trans-Volga. From the Volga to the Ural river, the southern border passes, apparently, somewhere along the latitude of Irgizi. The otter extends along the Ural [river] to the [Caspian] Sea.

From the mouth of the Ural, the border rises northward along the river and then turns to the east, including also the lower Ilek. The farther course of the border is entirely unclear and may be designated only tentatively. It bends around the Urals [mountains] along the Ural river and, after rising somewhat to the north, it passes somewhere along the border between the forest and forest-steppe zone, or along the forest steppe eastward to the Irtysh, and along it upstream to its sources (recorded at Ust'-Kamenogorsk and Chernyi Irtysh; Sludskii, 1953). It cannot be excluded that in the cut-off section mentioned, before the Irtysh, the line of the border passes somewhat more to the south—there is information on the occurrence of otter to the southwest of Petropavlovsk and to the west of Kokchetav (Sludskii, 1953), and, perhaps, even in the upper Ubogan river at Kushmurun Lake to the southeast of Kustanai (V.G. Heptner).

Beyond the Irtysh, the otter is absent in the Barabinsk, Kulundinsk and Cis-Altai steppes. In this zone, the border of the range, proceeding somewhat to the north of Lake Chana, reaches Ob' south of Novosibirsk, then goes directly south and, passing around the Altai from north [to east], reaches the Irtysh.

From the Zaisan depression and southern Altai to the Pacific Ocean, the range passes to the south outside the boundary of the USSR.

The range of the otter in Middle Asia is very narrow and complex. Moreover, its distribution is sporadic and it is everywhere rare. Locally, the otter is encountered only as a transient and has been observed or caught once in several years. In some regions where it occurred in the past, this animal is absent at the present time. Finally, data for Middle Asia are in general very scarce, fragmentary and in part indefinite. Therefore, it is almost

impossible to outline a more or less accurate range in this region at the present time.

The Middle Asian range of the otter must be considered as the northern edge of the Near Eastern part of the general range of the species, and in part, perhaps, the Central Asian (Pamir-Altai and Tien Shan, and Semirech'e). There is no direct connection with the main European-Siberian region of occurrence of the species in the USSR (between the Dzhungarsk Alatau and Chernyi Irtysh otter are absent), or it is weak and may exist in some form in the east. This is demonstrated by the systematic peculiarities of the northern and southern otters (see below).

In the west, a small section of otter occurrence is occupied by the Kopet-Dag [mountains] and Atrek [river] to its mouth. This is the northern edge of the Iranian part of the range, included within the limits of the USSR from the south. Another analogous section, isolated in our country from the first, is situated along the Tedzhen river, occupying its upper and middle courses and not reaching Tedzhen city. A third section is occupied by the Kushku river, where, as possibly in some sections of the Tedzhen, the otter apparently occurs only as a transient from the south, and extremely rarely (V.G. Heptner). Concerning the occurrence of otter on the Murgab, at the present time or in the past, positive data are absent, though it is not excluded, at least for its upper course.

Farther to the east, the section inhabited by the otter is, obviously, connected with Afghanistan, occupies the western Pamir; i.e., the region of rivers flowing from the east to the upper Pyandzh (Rozanov, 1935), Pyandzh [itself] and the uppermost Amu-Dar'ya and the basins of the rivers flowing into it from the right, in particular the Surkhandar'ya, Kafirnigan, Vakhsh-Surkhab, Kizyl-su and smaller rivers-Varzob, Khanak', Ilyak (Flerov, 1935; Chernyshev, 1958; V.G. Heptner). In the basin of Surkhandar'ya, the range includes the regions of the Tupalang and Sangardak rivers (Ishunin, 1962; V.G. Heptner); i.e. the southwestern part of the Gissar range. Along the Amur-Dar'ya, the range does not reach 865 beyond Termez. Concerning the occurrence of the otter in the remaining part of the Amu-Dar'ya, data are absent, and apparently it does not exist along this river. The extreme turbidity of water probably prevents its occurrence.

The otter is absent in the eastern Pamir. Concerning all remaining parts of the Pamir-Alaisk montane system with its water

bodies, we have no definite data on the occurrence of otter, except one reference to its occurrence on the Zeravshan below and somewhat above Samarkand (Fedchenko, 1950; Ishunin, 1961).

In Semirech'e, in the Tien Shan system and in the Syr-Dar'ya basin, the range of the otter occupies Dzhungarsk Altau and the region to the north of it to the Alakol' and Sasykkol' (basin of the Tentek river), the Karatal basin, the Ili basin and, apparently, other rivers flowing into [Lake] Balkhash; Kungei-Alatau (at least the northern slopes of its eastern half), Zailiisk-Alatau (in particular, Chilik basin), and the Chu river to its lower reaches (Sludskii, 1938, 1939, 1953). The otter was recorded in the Syr-Dar'ya in its lower course and for Chatkal [range] (Zarudnyi, 1915; Kuznetsov, 1948; Sludskii, 1963). Some of the data mentioned refer only to the past, and at the present time in the otter is, apparently, absent from a series of places.

For the entire remaining parts of the Tien Shan system, Fergana and adjacent places, southward as far as Surkhandar'va and the Pamir, and westward to Samarkand there are no definite positive data on the otter's presence. There is only vague and indefinite old information about occurrence of the otter in the lower reaches of rivers flowing into Issyk-Kul' (N. Severtsov, 1873) and for Przheval'sk [city] (Kuznetsov, 1948). There are even data, that in the past the otter was distributed throughout Kirghizia (i.e., through the entire Tien Shan system, in the Alaisk range and Alaisk valley), but by the beginning of the current century, it was "almost destroyed", although, "it is possible that it was somewhere still preserved" (D. Dement'ev, 1938). Equally, there are direct references about the otter's absence in Kirghizia (Kuznetsov, 1948). At the same time, the ecological conditions permit at least sporadic occurrence of the otter almost everywhere in the mentioned mountain system. One may think that, in the past, the otter's natural range occupied the whole Tien Shan and Pamiro-Alaisk districts, except for such places as the western Pamir where conditions of life for this species are unfavorable.

The otter's distribution is more or less sporadic almost everywhere. In forest-steppe and steppe districts of the above outlined northern range, there are, moreover, areas where the otter is completely absent (see for instance, Grigor'ev and Egorov, 1964). The otter nowhere occurs in great numbers and moreover, at the periphery of the range, but also in some regions far from the

periphery, the animal sometimes disappears for a considerable time and then appears anew. Local and long-distance transgressions may occur, as mentioned previously.

Geographic Range Outside the Soviet Union

This occupies all of Europe, to the west including Ireland, on the north the northern part of the Scandinavian Peninsula. On the Balearic Islands, Corsica, Sardinia, Crete and Cyprus, the otter is absent. The range farther includes northwestern Africa (Algeria and Morocco), Asia Minor, Syria, Palestine, more northern parts of Iraq except central and southeastern desert areas, Afghanistan, Kashgaria, parts of Tibet (details unknown; apparently those connected with Himalayas), Kashmir, Himalayas and northern India to the north of the Ganges. Southern India and Ceylon form a separate region of otter occurrence. In the central parts of India, L. lutra does not occur, and therefore, the range of this species here, like the ranges of the kharza [Charronia] and thar, Hemitragus) are disjunct. The northern border of the range of the southern Indian race (L. l. nair) is not accurately established. In Central India, Lutra (Lutrogale) perspicillata lives.

Farther, the range includes Assam, Burma, the Indochinese Peninsula, Malacca, Sumatra and Java. In Asia, the range includes, moreover, the Mongolian Republic (mainly the northern and montane parts of the country), northeastern China (former Manchuria), the greater part of the rest of China (except the steppe and desert regions), Japan, Taiwan and Hainan.

Within the limits of the outlined region of otter occurrence outside our country, there are considerable expanses where this species is absent. Thus, it is absent in the greater part of the deserts of Central Asia; apparently, in the greater part of Tibet, etc. Details are, however, unknown. In some parts of the range the otter has been exterminated (V.H.).

Geographic Variation

Although the otter's range is vast, it is remarkable that its geographic variation is very small. It is greater in South Asia, although one may think that presentations of it (for example, Pocock, 1942; Ellerman and Morrison-Scott, 1951) are nevertheless over-

866



Fig. 315. Species range of the otter Lutra lutra L. V.G. Heptner.

estimated. Increase in variation along the southern edge of the range in Asia is manifested both in the number of forms and also in the degree of their separation. Thus, for example, the characteristics of Java otters, *L. (L.) l. barang* (material of Z[oological] M[useum of] M[oscow] U[niversity]) in structure of not only the skull but also dentition are so considerable that, from a purely morphological point of view, they are analogous to specific characteristics. It is characteristic that all the southern "border" forms of Asiatic otters (*nair*, *barang*, *chinensis*) are small, while on the whole, geographic variation of Eurasian otters reflects Bergman's Law well. A certain decrease in dimensions southward is also noticed within the boundary of the USSR, but it is very weak.

Himalayan otters (monticola, kutab) do not differ in dimensions, 867 or differ very slightly only, from the northern otters. Moreover, in the south, there has been observed in places lightening of general color and of the relative color of the venter especially of neck and throat; i.e., increased contrast between the upper and lower body.

Geographic variation of otters in the Old World is still completely insufficiently studied. This also applies to the territory of our country. Descriptions of separate races have been done on very little material and have not subjected to serious revision. For the USSR, the following forms may be preliminarily accepted:

1. Northern otter, L. (L.) l. lutra Linnaeus, 1758 (syn. vulgaris, baicalensis, amurensis, kamtschatica, steinegeri).

Dimensions and mass relatively larger.

Color of back and sides dark-tawny, color of ventral surface relatively dark. Underfur silvery, with dark chestnut-colored hair tips. Pelage close-fitting and soft.

Whole range within boundary of the USSR except the northern Caucasus, Trans-Caucasus and Middle Asia, and southern and southeastern Kazakhstan.

Outside the USSR—in Europe, Mongolian Republic, northeastern China (former Manchuria), Japan.

The above given species description applies to this form [p. 1289]. It retains its principal characteristics in the whole huge expanse mentioned and under all the diversity of conditions in which it exists. Thus, even the separation of the Kamchatka otter as a separate subspecies did not receive approval. Furriers within the outlined limits also do not distinguish separate fur types, noting only that skins obtained from Yakutiya and from the Far East are of particularly high quality—of darker color and have very dense underfur. The entirely weak variation in otter of northern Eurasia is, apparently, associated not only with the fact that it is an aquatic form but also with its ability to settle in new and quite distant places.

2. Caucasian otter, L. (L.) l. meridionalis Ognev, 1931.

Dimensions and mass relatively less large.

Color of back and sides lighter than in northern form—light tawny. Ventral surface also somewhat lighter. Tail monotone both above and below. Underfur silvery with yellowish tint and light tawny hair tips. Pelage less close-fitting, somewhat coarse.

Body length (14) 530–710 mm; tail length 340–470 mm; length of hind foot 115–135 mm; ear length 20 mm. Weight 3.7–8.5 kg (adult individuals from Okum' river basin in western Trans-Caucasus and Kura; M.P. Pavlov, 1964).

In northern Caucasus and Trans-Caucasus.

Outside the USSR—in Iran, perhaps Iraq, Syria, Palestine and parts of Asia Minor.

This is a well-distinguished form, but still poorly studied. Individuals from Trans-Caucasus are quite typical, and northern Caucasian population comprises some numbers of more darkly colored individuals; *i.e.* it bears characters transitional to the northern form. Distribution outside the borders of our country are entirely unclear. Systematic and geographical relationships of this form to the following one are unclear (see below); nevertheless, affiliation of the Trans-Caucasian otter with the southern group of forms is evident. Its range, moreover, if not completely, then perhaps to some degree may be isolated, from that of the northern form by the steppes of the Cis-Caucasus. One may, apparently, consider that this isolation is greater than that from the southern parts of the species range.

3. Middle Asiatic otter, L. (L.) l. seistanica Birula, 1912 (syn. oxiana).

Dimensions similar to preceding form. General color is lighter—back is grayish-light tawny, usually with gray hairs; sides lighter than back, the belly very light whitish-yellow or whitish-gray. Sometimes has yellowish tone lightening throat forming a distinguishable patch variable in size and color. The tail is bicolored—upper like back and lower a light dirty-yellow-white. Pelage is coarse and not very close fitting.

In Middle Asia, on northeast including Dzhungarsk Alatau; possibly also region of occurrence in Turkmenia.

Outside the USSR-in eastern Iran and Afghanistan.

This form is well differentiated from the northern, although among the described type in the population are dark individuals with fur color and characteristic very similar to that of the northern form, especially in the mountains. It is very similar—if not identical—to the Trans-Caucasian form to it. Together with it, they themselves represent members of the group (its size not clear) apparently of the Near Eastern type distributed along the southern edge of the western half of the country's Asian part. Ranges of the

Trans-Caucasian and Middle Asian form (meridionalis, seistanica) in their northern section are, to a considerable degree, quite fully isolated from southern regions inhabited by the nominal form. This applies to the Cis-Caucasian steppes, steppes of Kazakhstan, the expanse between the Altai where the nominal form lives and Dzhungarsk Alatau occupied by the Middle Asiatic (Sludskii, 1953). If the otter's range in the Near East were not so limited, one could assume that forms of this type have settled (penetrated) with us from the south. The group of otters mentioned is analogous to the southern group of races of brown bear—isabellinus-syriacus.

Systematic and geographic relationships between the mentioned forms are not clear. They are described from quite nearby places (lower Gilmend-Tegeran) from very few materials, having similar characteristics. It cannot be excluded that, in the future, with accumulation of new material, these forms may be united. Also not clear is the relationship, at least of the Middle Asiatic form, to the other adjacent races described from the Himalayas and northern India. The forms *monticola*, *aurobrunnea* and *kutab* were described from Nepal (first two forms) and from Kashmir respectively, and were also recorded in Kashmir and Punjab; *i.e.*, in those places nearest to our southern Middle Asiatic regions in part directly neighboring (Kashmir).

Leaving aside the problem of relationships among the listed Indian forms (they are hardly entirely independent), one may be assured with great likelihood that our Middle Asian (at least Pamiro-Alaisk and Tien Shan) otters are related to them. Apparently, they must bear the name of the Kashmir form *kutab* (if it is separate from *monticola*, which is quite doubtful).

One must also keep in view that the form seistanica was described from the delta channels of a river which disappears in the hot lowlands on the border of Iran and southern Afghanistan, while all the other named races were described from montane countries. The name seistanica was left here, therefore, conditionally, as a traditional one in our literature until direct comparison of our material with Indian, and revision of all Himalayan and northern Indian forms. Published data (Pocock, 1941) give a completely confused picture both of systematic and geographic relationships. It seems highly probable that otters of the Himalayas and the Middle Asian mountains, at least to the east of Amu-Dar'ya, all belong to one form, which should be designated by the name monticola. It is

possible that the name *seistanica* may be related to the group *kutab*, perhaps in the form of a synonym.

Outside the boundaries of USSR, the following forms are accepted: 1) L. (L.) l. angustifrons Lataste, 1885—Algeria, Morocco (possibly a synonym of the nominal form); 2) L. (L.) l. chinensis Gray, 1837—continental China, except Tibet and northeastern China (former Manchuria), Taiwan, Hainan; 3) L. (L.) l. monticola Hodgson, 1839—northern India (Punjab, Kumaon, Nepal, Sikkim, Assam); 4) L. (L.) l. aurobrunnea* Hodgson, 1839—Nepal (the most elevated parts), Garhwal (apparently, a synonym of the preceding form); 5) L. (L.) l. kutab Schinz, 1844—Kashmir, and to Tibet (probable synonym of the form monticola); 6) L. (L.) l. nair F. Cuvier, 1823—southern India and Ceylon (a well-distinguished form); 7) L. (L.) l. barang F. Cuvier, 1823—Sumatra, Java, Malacca, Indochina (a sharply-expressed race) (V.H.).

Biology

Population. The otter belongs among a number of low-density animals. In the past, when exploitation did not yet considerably affect the status of its stocks, the annual yield within the boundary of the USSR was 5000 otters, over the course of a series of years. Annual growth of this animal ranges from 20 to 30%. Taking into consideration the absence of overhunting at that time, it may be assumed that the number of otters in the USSR did not exceed 20,000 individuals, falling to about 10,000 in years of more intensive hunting. The smallest number of otters is in Siberia, while in West European countries, in spite of the predominance of cultivated lands and intensive settlement of the territory, it is more frequent than in the USSR. The yield from the USSR constitutes 10% share of the global one, that of West Europe—a 25% share of the skins; the cause of this is the fact that otter populations are most of all limited by the character of the ice regime of water bodies.

The otter is distributed throughout almost the whole USSR, but very unevenly. Its range is not continuous, but forms a sort of net, which is generally characteristic of all animals closely associated with fresh water. Density of river distribution determines, first of all, density of the otter occurrence. However, there are

^{*}Misspelled aureobrannea in Russian original-Sci. Ed.



869 Fig. 316. Habitat of otter in Altaisk preserve. Lower Chul'chya river. Photograph by G.D. Dul'keit.

other very essential causes limiting the number of otters and the density of settlement in fresh waters of the USSR.

Habitat. The otter is a true freshwater animal. It usually 870 captures food in water, and here also takes its shelter in case of danger. It usually only comes ashore to rest. The otter inhabits freshwater bodies in all landscape zones. It also lives on the seashore where it even becomes frequent locally, but usually only in the mouths of rivers, or even creeks. Height above the sea level, characteristics of relief and geographical latitude, as well as the direct influence of climate are of no importance to otter in the presence of other favorable life conditions. Where the otter is not intensively hunted, it does not avoid the densely populated places or even the neighborhoods of large cities. In Middle Europe, cases are known of otters even living in city. On the whole, the number of otters is inversely proportional to the number of hunters. For the same reason, numbers of otters usually increase parallel to increasing afforestation of a place.



870 Fig. 317. Habitat of otters in "Kedrovaya Pad'" preserve, southern Primor'e.

May 1963 (Photograph by A.G. Pankrat'ev).

The characteristics of river banks and their relative inacessibility to humans are very important for occurrence of the otter. Almost impassable wooded banks, reed thickets and turgai, and general inaccessibility of the shore zone from land, are favorable for it. Because of this, the otter evidently often prefers forest rivers, with greatly cluttered channels choked with obstructions and broken twigs and branches which make these rivers impassable not only for boats, but also for a walking person. In spite of the fact that the nature of these rivers hinders the otter itself in catching food, it settles willingly in such rivers.

Rivers with transparent waters, rapid flow and rocky beds are preferred by otters to water bodies with slow flow and polluted water, muddy bottoms, matted water plants and opaque water although it also settles in such bodies. All of this is related to conditions for catching food. Abundance of its food is also very essential: of deciding significance is the abundance of fish in the water body. One of the main conditions in the otter's ecology also proves to be the character the water and snow regimes of the water



871 Fig. 318. Winter aspect of otter habitat on Teletsk lake in Altai preserve. Tracks of otter (here also tracks of kolonok and American mink). Photograph by G.D. Dul'keit.

body in the winter period. The presence of *polynias* [open water], thawed patches, ice holes, and "spring places"—opportunities for otters to penetrate into the water and catch food there—are necessary for the otter.

The feeding possibilities in unfrozen sections of water bodies are usually limited, and therefore open areas under ice, which are formed during winter reduction of water [level] are of no less importance to otter. This gives it the possibility of finding food

under the ice without coming out onto the surface and in this way, the significant part of the water body being utilized is extended. With the freezing over or complete freezing of the water body, it is not suitable for the otter in winter. The impregnable ice cover and the rarity of unfrozen sections practically deny the otter the possibility of exploiting even those rivers richest in food. Prolonged ice cover is also unfavorable for these animals.

Food. Vertebrate animals, and above all fishes, everywhere predominate in the food of the otter. Frogs, birds and mammals sometimes play an essential, but strictly seasonal, role. The significance of invertebrates is small—these are mainly large water beetles. Locally, crayfish and freshwater mollusks have some significance. Consumption of plant food has been noted only for otters held in captivity.

In the fish-rich channels of the Volga delta, the frequency of fish in the otter's diet constitutes 88% on average for the year. In the warm period of the year, it remains at a level of 91.6-97.6%, but in winter falls to 55.6%, while during the period when water body are frozen, and because of great difficulty of their capture at this time—to 27%. Among all fish eaten at that time, cyprinids constitute 60.2%, carnivorous fish—23.6%, and sculpin—10.7%. Fry, eaten avidly, constituting about 1/3 of all fish. The otter prefers small fish to large. In first place in frequency stands the carp (33.8%), constituting 25% of all fish eaten; in second place—pike (24.3%); in third—roach (18%); followed next by sculpin (13.2%) and shiner (11.6%). Many other fish are encountered, but in small amounts (403 samples; A.G. Romashova).

In the upper Pechora, the proportion of fish in the diet constitutes about 65% annually, fluctuating seasonally from 58% (summer) to 74% (spring). The significance of fish here is less than in the Volga delta. Grayling (24.2%), rock sculpin (26%) and loach* (13.4%), i.e. rheophilic forms, predominate, constituting on the whole 79% of fish eaten. Of these 43% are pelagic species, and 57%—bottom [fish]. Limnophilous forms constitute only 21%, including only 4% bottom [forms]. This is explained in that the otter prefers water bodies with fast transparent water where it is easier to catch fish. Inhabitants of deep water-whitefish, ide, are rare here in the otter's diet, and, as in the Volga delta, small fishes

^{*}The Russsian word "golets" can mean either loach or brook trout-Sci. Ed.



872 Fig. 319. Pra river in Oksk preserve (Ryazan district)—habitat of otter. Complete ice cover. Path of otter (trench) along deep trail at -42°C. January 1950. Photograph by V.G. Heptner.

(weight to 200 gm) and fry predominate. Large fish weighing more than 1–2 kg are rarely met with; in individual cases, capture of burbots weighing up to 4 kg were recorded. Pikes are not often caught, especially small ones not more than 10 cm long. Commercial species constitute 45.5% (1530 specimens; Teplov, 1953).

In the Lapland preserve (Kola Peninsula, Kislaya river basin; 414 samples—261 excrement in summer, 38 in autumn, 115 in winter; Vladimirskaya, Lebedev and Nasimovich, 1953) fish also

occupies first place in the otter's food. In the yearly cycle, brown trout predominates (35.5%), followed by pike (15.2%), burbot (15.1%), whitefish (10.8%), grayling (8.1%), minnow [*Phoxinus*] (7.8%), and perch (5.8%). Riverine species predominate over lake forms and constitute 78%. Small fishes (up to 20 cm long) constitute 70.2%, and large—29.8%. Only 4.4% were more than 50 cm long. The otter begins to eat large fish in the trunk region. In summer, fish constitute 23.6% of the otter's diet, in autumn—5.3%, and in winter—29.6%.

The otter feeds on grass frogs mainly in winter (29.6% occurrence) when it does not have adequate food. It obtains them from the bottom of small unfrozen rivulets. In summer, it catches them along the river banks and in swamps (23.6%). It occasionally feeds on ducks (teal, golden-eye) and mammals (voles, water shrew, squirrel) in isolated cases. Among insects, in winter it feeds mainly on caddis flies (12.2%) and stoneflies (8.7%), and in summer—ground beetles (2.6%). Among mollusks, it eats primarily *Anadonta* (1.5%) in small numbers.

In the Altai, fish constitutes 95.9% occurrence in the otter's food, and the larvae of caddis flies—83.6% (Ternovskii, 1956).

In general, the species composition of fish in the otter's food depends on the composition of ichthiofauna of the given water body and the vulnerability of each species. In Caucasus, brown trout, barbel, Chondrostoma and others predominate. In forest rivers of the Volga basin, the otter feeds in winter mainly on burbot, and in summer on other bottom fishes. On the Murmansk coast, it feeds on cod, salmon trout and others. In the otter's diet, frogs are a typical winter food, exhibiting sharp seasonal fluctuations. In the upper Pechora, the average annual frequency of occurrence is 18%, fluctuating from 10% in spring to 26% in winter (Teplov, 1953). In the Volga delta this fluctuation is sharper—from 2.4-3.5% in the warm period of the year to 46.1% in winter and 69.2% in 874 periods of complete freezing of the water body. It is a very important food for otters in winter, but by no means a preferred food. In spring, frogs are numerous in the Volga delta, but the otter hardly catches them at all. It only hunts them under ice in their hibernating places where up to 1156 frogs may congregate per 1 hectare (A.T. Romashova). On the Pechora, in the warm period of the year, the otter feeds more intensively on frogs (10-18%). Here, the



873 Fig. 320. Polynias [open water] in Kedrovaya river—the otter's place of permanent residence in winter. "Kedrovaya Pad'" preserve, southern Primor'e. December 1963. Photograph by A.G. Pankrat'ev.

water bodies are less rich in fish and conditions for capturing them are, apparently, also less favorable.

The significance of birds in the otter's food varies greatly. In the upper Pechora their average annual frequency is 13%. In the Volga delta, in spite of the abundance of birds, is two times less—6.1%. In the upper Pechora in summer, birds comprise 26%; among

them, ducks—7.9% and snipe—6%. Ducks of open waters are encountered somewhat more often than those species which confine themselves to dense growths of water plants. In the Volga delta in summer, frequency of birds reaches only 1.8%, but in this case, not ducks, but to coots and their nestlings. Cases of otters hunting moulted ducks are very rare—the birds restrict themselves to places unfavorable for hunting by the otter. Apparently the increased frequency of frogs and birds in the food of the Pechora otter is associated with small numbers of fishes.

The mammals represented in the otter's food are mainly water voles [Arvicola], less frequently water shrew [Neomys] and still more rarely, other species which can appear on the shore of the water body or may swim across it. Due to local conditions, the significance of water voles varies. For example, in the upper Pechora, depending on the season, the percentage of occurrence ranges from 2 to 5%, and in the Volga delta, reaches 12% both in summer and in winter. During the period of complete freezing, it then increases to become one of the major sources of food—19.2%. Complaints have recently appeared that the otter in the Ural [river], noticeably affects the number of muskrats (Bakeev and Koryakov, 1960).

The daily ration of the otter consists of about 1 kg of fish. When constantly supplied with food, the otter eats during a night 0.4–0.9 kg of fish, in the breeding season—0.2–0.4 kg, and after prolonged starvation—up to 1.5 kg. (A.T. Romashova). Feeding on small fishes, the otter becomes satiated overnight with 2–3 helpings, and with a large catch—after 1 helping. It is curious that one water vole of about 145 gm can fully satiate it (A.T. Romashova). This is probably conditioned by the higher nutritional value of warm-blooded animals in comparison to fishes.

Home range. The home range of the otter is limited in width to the narrow [river] bank zone—not wider than 100 m on each bank. Depending on the food capacity of the water body, the home range may be unitary or consisting of a series of separate ranges, separated from each other by non-feeding areas. The length of the section and its area depends also on the abundance of food and conditions for its capture. The separate feeding sections may form a chain extending for 15–20 km along the course of one river, or the otter may periodically visit a series of adjacent lateral tributaries, reaching them by way of their mouths or crossing the

watersheds on land. In water bodies with abundant food, the otter leads a settled life in a section extending from 2 to 3-5 km. In the great taiga rivers of the Pechora basin, the average length of the home range for a series of years was 6 km (Teploy, 1953). Therefore, the area of the range inhabited by the otter fluctuates from 4-12 to 300 hectares. On the Kola Peninsula, the otter covers 4-6 km in 24 h period and sometimes more (Vladimirskaya, Lebedev and Nasimovich, 1952).

In winter, when roaming around the watersheds, and also with strong freezing of water bodies, the otter moves along snow and river ice 15-20 km per 24 h period. On the Kola Peninsula, leading almost a migratory mode of life in winter, the otter commits a transgression into a neighboring section 20-30 km in length and sometimes including neighboring rivers and creeks. On ice, it moves up to 15 km, and on snow, up to 8 km per 24 h period.

Burrows and shelters. Within the boundary of the home range. the otter usually has a permanent burrow, and also a series of temporary shelters and hiding places. The latter are entirely vari-875 able depending on local conditions. These may be eroded areas of steep banks protected by tree-roots, heaps of driftwood and fallen branches, and caves in the rocky shore, etc.

The permanent burrow is often constructed in a steep, although not high, bank. Its entrance opens under water, at a depth of 0.50-0.75 m. The sloping passage, 1.5-2 m long and about 20 cm in diameter, leads to a nest chamber 0.4-0.5 m in diameter, often lined with dry grass or moss. In one case, it was found at a depth of 20 cm from the soil surface (Teplov, 1953). In the family burrow, the nest chamber is always located so that it may be submerged only during spring flooding. During that period the otter, like the beaver and desman, is deprived of permanent shelters. In low-lying places where high level of groundwater does not permit construction of burrows, the otter builds a shelter for the litter of young in high piles of reeds or fallen branches, in the heaps of driftwood half-covered by sand and silt, flotsam,* and other cover. In well-protected places, the otter sometimes gives birth to its young. even on the surface, but does so in a carefully concealed nest—a lair.

^{*}In the Russian original this word is misspelled "plavnik" (fin, flipper) instead of "splavnik" (flotsam)-Sci. Ed.

In winter, in Anadyr Territory, the otter sometimes settles in a shelter under a steep overhanging bank which has an exit to the sub-ice space. Its activity is thus hidden to a considerable degree from the eyes of observers. On Kola Peninsula, otter forms occur under snow, rarely on the shore or on snow-covered rocks. "The dining room" is located on rocks which have on one side an edge sloping to the water. "Latrines" occur under spruces with the crown hanging near ground, usually directly on ice (Vladimirskaya, Lebedev and Nasimovich, 1953).



875 Fig. 321. Shore rocks with niches and clefts—shelters of otter in the course of the entire year "Kedrovaya Pad'" preserve, southern Primor'e. May 1963.

Photograph by A.G. Pankrat'ev.

Daily activity and behavior. The otter leads mainly a crepuscular-nocturnal mode of life. It is especially active on moonlit nights. In places where it is not disturbed, it sometimes also appears during the daytime; this more often occurs in winter than in summer. Increase in diurnal activity in winter sometimes manifests dependence on diminished conditions of illumination under the layer of snow and ice, which hinders the otter in catching fish at



Fig. 322. Winter shelter of the otter on an eroded bank. A bunch of dry grass at the edge of an ice-free area, which the otter was carrying to the shelter, and dropped upon the approach of a human. "Kedrovaya Pad'" preserve, southern Primor'e.

January 1961. Photograph by A.G. Pankrat'ev.

night under the ice (Teplov, 1953). On the Kola Peninsula, it is active round the clock (Vladimirskaya, Lebedev and Nasimovich, 1953).

The otter leads a secretive mode of life. It hunts, by waiting for its prey on shore, or by pursuing it. Obstructions in the water body, a silty bottom, unclear water and growth of water vegetation hinder capture of food by the otter, but at the same time increase the protected nature and safety of the habitat.

On dry land, the otter is clumsy and less mobile, but has endurance, and even in deep snow, progresses for ten kilometers or more. No dog at all can overtake the otter, even following fresh tracks. In water, the otter is very quick, dexterous and mobile. It catches large fish, by diving under them, seizing the abdomen, or rarely taking the back. It may happen that a very large fish pulls away from its teeth and escapes with wounds (A.T. Romashova). Diving under the water, the otter is at first not evident, but then its path may be followed by the bubbles exhaled when it breathes out. For breathing, when there is danger, the otter sometimes thrusts only the tip of its nose to the surface. Sallying out of the otter onto shore most often occurs in definite, well-concealed places, and usually they have the character of beaten tracks, similar to those of the beaver. In some places, so-called "otter slides"* occur. These are smoothly polished, well-beaten paths on steep slopes of the bank, often damp and slippery. There are observations that otters "amuse themselves" by sliding many successive times along these steep tracks into the water. Moving along the surface of the ice, the otter quite often, making a running jump, slides along on its belly, leaving a long trough-like track. Such behavior in the otter, as in mink, is explained by the need to dry the wet fur (Ternovskii, 1956).

The otter mainly hunts "stationary" fishes or those slowly swimming. It also hunts at "fishing holes" and hunts fry on small bars. When hunting, the otter swims with its head and part of its back on the surface. After seeing its prey, it dives.

877 Otters usually live singly. However, females and their litter stay together for the whole autumn and winter, and usually remain with it until mating again. The female defends and protects the litter, and the male, apparently, sometimes participates in its upbringing.

^{*}Literally, "sliding hills" in Russian original-Sci. Ed.

Seasonal migrations and transgressions. The otter is an extremely mobile animal. However, its frequent wanderings, from one water body to another, giving the impression that it is migratory, nomadic animal, actually take place within its home range. These wanderings are explained by water bodies becoming food-deficient especially in winter, with an unfavorable ice regime, the home range occupies a considerable length of shoreline. Neither can the otter's crossing of watersheds be called migration. These also bear the character of movements within a vast home range.

Reproduction. Reproduction in otters is still very insufficiently studied. A series of contradictory points of view exist. These, as well as the existing facts, may be harmonized according to the existing level of our knowledge in the following way. 1. As in many species of the mustelid family, there is a latent period in embryonic development in the river otter. The duration of this period is completely unstable and is determined by environmental factors. In several sections of the range, the latent period is liable to individual fluctuations and in others—it is more or less stable and is. at the same time, different in different sections. After the end of this period, pregnancy apparently proceeds for about 60 days without deviation. 2. Corresponding to variations in duration of the latent period, the times of estrus and mating are subject to some deviations. Most frequently, apparently, estrus and mating take place during March and last about one month. This applies to the Volga delta region (A.T. Romashova), Mari Republic (V.A. Popov), upper Pechora (Teplov, 1953) and southwestern Kalinin district (P.B. Yurgenson). The date of beginning of this period is changeable (February-April).

On the other hand, there are reports of otter cubs of one and the same age (one month) found in June and October–December. Quite well-developed embryos were found in otters caught in January. In February, an otter cub the size of a domestic cat was taken. Such dimensions of young were attained both in January and July. An otter cub which could hardly walk was once found on the snow (A.T. Romashov). The data obtained from the tributaries of Amur also confirm that otters reproduce at any time of the year—"like dogs". There is a report that in the Caucasus, estrus in otters occurs at the beginning of winter. For the Volga delta, the possibility of mating in times other than March is not excluded, but such exceptions are rare. Late litters usually die in winter. Parturition

occurs here in June-beginning of July. In the upper Pechora, it occurs at the end of April-beginning of May, and in June active young otters are observed. On 18 June, two young males were caught, with the eyes opened, but the teeth had barely erupted (weight 1 kg, body length 33.5 cm; V.P. Teplov). Most often, births occur in May. Previously mentioned differences in dates serve as adaptations to the local ecological conditions. The number of young in the litter varies from two to four. Individual cases are known when there were 5 otter cubs in a litter (Khorol river, Ukrainian SSR). In the upper Pechora, no more than two otter cubs were observed in litters. The number of young is closely related to the degree to which environmental conditions are favorable.

In England, the newborn cubs are encountered at any time of the year, not excluding winter (Stevens, 1954). In one region the majority of births took place late in autumn and in winter (October–February), and in others—in the period from January–February to April inclusive. In 134 cases (for several years), the occurrence of new-borns was distributed by months of the year as follows: January—14; April—10; July—11; October—12; February—8; May—11; August—13; November—11; March—10; June—11; September—11: December—12.

In the British Isles, winter is mild, and the otter is not subject there to sharp seasonal fluctuations in conditions of existence. In captivity, estrus in the female is repeated each month until mating is productive. Mating is accompanied by a sharp whistle produced by males. At this time, a fight may occur between them. Pregnancy lasts 61–63 days. Duration of the latent period is variable and may be more than 9 months.

Growth, development, and molt. Data are few and fragmentary. Young animals are born blind and without teeth, with short dark underfur. They begin to see at the age of about 35 days (Stephens, 1954). In the female, there are three pairs of nipples; however, usually only a part of them functions. Young females gain in dimensions and weight more slowly than males. Young otters gain about 400 gm in weight each month, and at 10 months weigh about 4 kg. At the age of one year, they attain the size (but not the weight) of adult individuals. Sexual maturity in individual cases (in captivity) is attained in the second year, and probably more often, in the third.



Fig. 323. Otter on the ice of a creek near an otter slide. "Kedrovaya Pad'" preserve, southern Primor'e. January 1961. Photograph by A.G. Pankrat'ev.

Molt in the otter proceeds very gradually, and is little noted. Enemies, diseases, parasites, mortality, competitors, and population dynamics. Other than humans, the otter has no dangerous enemies. Neither has it any serious competitors. It usually forces out mink from the borders of its home range, often destroying them. On the Kola Peninsula, the wolverine was referred to as an enemy of the otter, and the white-tailed eagle as a competitor (Vladimirskaya, Lebedev and Nasimovich, 1953). Beaver activity is usually useful for the otter—in winter the latter uses beaver outlets from under the ice. Diseases of epizootic character are unknown. In captivity, coccidiosis infection has been recorded. In a severely emaciated otter killed while attacking a domestic goose, pulmonary tuberculosis and endocarditis were diagnosed (Stephens, 1954). Helminth infections are not major.

The main cause of mortality, especially up to one year of age, is unfavorable weather conditions in winter, in particular, the ice regime. Late litters usually die in winter. In the upper Pechora, a connection exists between the survival of young, magnitude of autumn flood favoring the formation of sub-ice spaces and the



879 Fig. 324. Track and prints of night life of an otter family—a female with young.

18 December 1964. Photograph by A.G. Pankrat'ev.

duration of the ice-cover period. The otter population there is determined by intensity of reproduction and survival of young. The average percentage of young in otter populations was 19.0, with variation from 12 to 26%, *i.e.* more than 2 times (Teplov, 1953, 1954).

The otter responds very quickly and positively to prohibition of hunting (launching)* with real observance of it. The cultivated landscape does not directly prevent the growth of the otter population if they are protected from direct pursuit and destruction. Only measures giving rise to impoverishment of the ichthyofauna of water bodies have proven to be harmful: floating forest litter, sewage drainage from industrial enterprises, etc.

Field characteristics. Sightings of river otter are rarely successful. It is difficult to confuse with any other animal. Tracks of otter, and their excrement are often encountered. The large tracks of this animal most often bear well-marked outlines of the swimming

^{*}Meaning of parenthetical word "zapusk", or "launching" not clear—Sci. Ed.

membrane between the digits. Its track is clearly separable from that of the beaver in that it usually extends along the bank at the edge of the water, while the path of the beaver is always perpendicular to the line of the bank—these are its sallies onto the bank.

Excrement of the river otter usually possesses a greenish tint, and is often watery. The remains of fish bones and scales of fish are typical of them. From mink excrement it differs in large size.

880 The otter usually leaves them [feces] on rocks in and around the water body or on the bank, as well as in holes on sandbars. It is often buried. Its urine typically has a strong odor peculiar only to it.

On snow, the otter leaves not only its footprints, but also the track of its dragged tail. In deep snow it makes a whole furrow with its body. On river ice, a long ribbon of a trail (sliding after running) is typical, as are tracks emerging from water.

The otter sinks into the snow for 10–15 cm; the length of its leaps equal 50–110 cm more often 60–80 cm; the length of the trail made sliding on snow is 2–3 meters (Vladimirskaya, Lebedeve and Nasimovich, 1953). The otter sometimes proceeds for up to 6 km along ski-tracks. The weight loading on 1 cm² of the foot surface is equal to 53.2 gm for the male and 37.4 gm for the female (Teplov, 1953). In the period of reproduction, the otter's presence may be revealed by whistle of males at night (P.Yu.).

881

Practical Significance

The river otter provides very valuable fur—beautiful, warm and durable. From it are manufactured fur articles in natural shape but with plucked guard hairs, or even dyed a black color as "sealskin". Such articles are usually sold as a "true seal".

The otter is not numerous and is captured in limited numbers, more or less occasionally and accidentally. At the present time, capture of this species is carried out by licensed trappers. In RSFSR, 6100–6700 otters were trapped by license in 1956 and 1957. The annual catch for the USSR was about 7.5 thousand for the same years. The world catch of otter before the Fatherland War [World War II] was 80–100 thousands.

Due to the small number of otters in the USSR, the harm from it to the fishing economy is negligible.

The otter is usually hunted with guns and dogs, more rarely by still-hunting on moonlit nights. Harvest by jaw-traps is of a certain



880 Fig. 325. Tracks of an old otter male on light, wet new-fallen snow on the ice. "Kedrovaya Pad'" preserve, southern Primor'e. March 1962. Photograph by A.G. Ponkrat'ev.

significance, but good traps for catching this animal are not available. All other methods are either not productive or are not allowed as inhumane.

The otter is easily tamed and capable of domestication, and after a more detailed study of its reproductive processes might be bred in captivity. This is, however, possible only where there exists abundant and cheap food (fish) (P.Yu.).



881 Fig. 326. Prints of hind and fore feet of otter on a sand bank and the scheme of arrangement of the tracks during different gaits. Neya river, Kostromsk district. 24. X-1950. Sketch by A.N. Formozov, about 2/3 natural size.

Genus of Kamchatka Beavers or Kalans*

Genus Enhydra Flemming, 1822

- 1816. *Pusa*. Oken. Lehrb. d. Naturgesch., 3, p. 985. Nom. praeocc. *Pusa* Scopoli, 1777, Phocidae.
- 1822. Enhydra. Flemming. Philos. of Zool. 2, p.187. Mustela lutris Linnaeus, 1758.
- 1827. Latax. Gloger. Nova acta phys.-med. Acad. caes. Car.-Leopold, 13, p. 511. Renaming of Enhydra Flemming, 1822.
- 1829. Enhydris, Fischer. Synops. Mammal., p. 228. Substitute for Enhydra Flemming. Nom. praeocc. Enhydris Merrem, 1820, Reptilia (V.H.).

Measurements very large—largest in the subfamily and family. General body construction heavy, trunk very long, cylindrical in form. Limbs short, hind [limbs] displaced backward. Foot flipper-like, paw of fore limb short, digits unsegmented externally. Tail muscular, its length constitutes one-quarter to one-third that of body.

Fur long and very dense. Color tawny and brown in tone. Externally, glandular areas at base of tail absent. Two pairs of teats, but only one functions in female.

Skull massive and heavy. It is high and broad, with facial portion strongly shortened and elevated anteriorly, and terminated nearly vertically. Postorbital constriction only slightly narrower than interorbital. Brain case short, but very wide. Mastoid width only slightly less than zygomatic. Protuberances and crests of skull sharply defined; not only occipital but also sagittal crests well developed.

Dental formula
$$I = \frac{3}{2}C = \frac{1}{1}P = \frac{3}{3}M = \frac{1}{2} = 32$$
, *i.e.* somewhat reduced.

Incisor formula 3/2—a rare exception among carnivores (one bear has 2/3). As a form of anomalous deviation, an additional underdeveloped lower incisor may be manifested. It is probable

that in milk dentition is
$$I\frac{3}{3}$$
.

*"Kamchatka beaver" was the common name originally bestowed by Russian fur traders. At present, the accepted common name in English is "sea otter," and it will be used in this account, together with the native name "kalan"—Sci. Ed.

Anterior premolars with obtuse apices, posterior premolars and molars are almost flat, with low, blunt, rounded apices. "Carnassial" structure of upper third premolar not expressed. It has a rounded triangular form, with one angle directed inwards. Upper molar considerably larger than last premolar, of rounded triangular form, one side directed forwards toward premolar and other side—inwards. First premolar only slightly shifted deeper into toothrow. Lower carnassial tooth not developed either. This is an extreme deviation in the family in the sense of loss of "carnassial" structure of the dentition formula, is also observed in badgers and otters (*Lutra*). Here, the cutting form of the tooth is entirely lost. Such a structure itself represents an adaptation to feeding on sea-urchins and mollusks.

Vertebrae 50-51 (C 7, D 14, L 6, S 3, Ca 20-21), thoracic region elongated and composed of 14 pairs of ribs, of which 10 articulate with sternum. Scapula broad with poorly developed acromian process; pelvis narrow and long, situated to a considerable degree parallel to vertebral column, humerus very massive, noticeably spirally twisted. Femur shortened.

883

Stomach relatively large, intestine very long (exceeding body length by approximately 10 times), gall bladder present. Ligamentum teres absent. Lungs relatively large, diaphragm lies obliquely: fixed more posteriorly on dorsal side than on ventral (characteristic feature of truly aquatic animals, associated with increased dimensions of lungs).

Testis located under skin (scrotum is not formed).

On the whole, in all of its morphological features, the genus *Enhydra* represents an extreme degree of specialization in the sense of adaptation to water, not only in the subfamily and family, but also in the order as a whole. From a purely biological and bio-morphological viewpoint, sea otters occupy an intermediate position between those types of aquatic mammals which are represented by pinnipeds and terrestrial mammals, standing in the series relatively closer to the former. Of course, the described genus must not be considered as genetically linked between these groups; however, it indicates one of the possible biological stages in the path of transformation of terrestrial mammals to aquatic.

A purely marine littoral form of temperate and cold temperate, and in part warm temperate waters, specialized for feeding on fish and marine invertebrates (mainly sea-urchins).

Distribution restricted to shores of the northern part of the Pacific Ocean, north from 23° N. lat. in the east and 40° N. lat. in the west.

The genus *Enhydra* is restricted very sharply, and stands apart from other genera of the subfamily, especially *Lutra* and *Pteronura*. In fact, differences from the genera *Aonyx* and *Paraonyx* are also just as sharp, and attempts to relate them are deprived of any basis. On the whole, the genus *Enhydra* contrasts with the remaining genera of the subfamily, each of which is nearer to one another than to *Enhydra*. It represents an extreme type, and a terminal link in the development and specialization of the otter group. Attempts to separate it even into a special subfamily have been made more than once.

The origin of the genus is usually associated with the extinct genus *Potamotherium* comprising several species (at least two) from the upper Oligocene and the lower Miocene of Europe. Connecting links between Potamotherium and Enhydra are not clear: in the mind of some authors (Pohle, 1919), for this may serve one of the fossil European species of the present African genus Aonyx (A. hessica); however, this is doubtful. The genus Enhydra is known from the upper Pliocene, when it was represented by the extinct species, E. reevei, in the North Atlantic (England). This species is considered the direct ancestor of the present kalan [sea otterl. It is supposed that in the Pleistocene, from the Atlantic, Enhydra colonized the Pacific Ocean (Pohle, 1919). It is entirely possible that the path of colonization was the sea washing northern Eurasia. Generally, the geological history of the genus is unclear, and there is a basis for assuming its earlier occurrence in the Pacific Ocean.

This is one of the characteristic species of the northern Pacific ("Beringian") center of development of aquatic and inshore fauna, in which are included such remarkable forms as Steller's sea-cow, *sivach* [Steller's sea-lion], and a series of bird species (black guillemots, cormorants).

The genus includes only one species: *Enhydra lutris* Linnaeus, 1758. One of the most valuable fur-bearing species. Its falls under full protection throughout its entire range (V.H.).

Enhydra lutris, Linnaeus, 1758

- 1758. *Mustela lutris*. Linnaeus. Syst. Nat., Ed. X, 1, p. 45. Commander islands².
- 1777. Lutra marina Erxleben. Syst. regni. anim., p. 445. North Asia and America.
- 1799. (1800) Lutra gracillis. Bechstein. Thomas Pennants allg. Uebers d. vierfüss Thiere, 2, p. 177. "Statenland"—one of the southern islands of Kuril chain, apparently Kunashir.
- 1816. Pusa orientalis. Oken. Lehrb. d. Naturgesch., 3, p. 986.
- 1827. Lutra stelleri. Lesson. Man. de Mammal., p. 156. Kamchatka.
- 1922. Enhydra lutris kamtschatica. Dybowski. Arch. Tow. Nauk. Lwow, 1, p. 350. Nom. nudum (V.H.).

Diagnosis

Only species of the genus.

'The true Russian name of this species must be considered "Kamchatka bobr" (more correctly bobior), or "sea bobr". The old popular name of the Bering Sea—"Bobr Sea"—was derived from this word. The name of the animal came into the language of literature through Pushkin ("Its bobr collar silvers as the frosty dust"). The word "kalan" somewhat modified from the word "kalakha" was used by Russian people only in the 18th century and then very rarely (Pallas, 1811). At the present time, because of the danger of mixing it up with the river bobr [beaver] (!), some zoologists use it in our literature. Following this "principle", evidently such names as "sea slon" (northern elephant seal) and "sea lev" (sea lion), "sea ezh" (sea urchin), "sea liliya" (sea lily) etc. must also be changed. The name "kalan" came into daily use, but must now be considered as artificial and bookish. It is not known there. Such is also the name "sea vydra" [sea otter] a translation from German.

Fur manufacturers name the young animal suckling still feeding on milk "medvedok" [young cub], the semiadult (1 year)—"koshlak", the female—"matka" [dam], and the adult male—"bobior, bobr" (=otter).

²The assignment of Linnaeus "habitat in Asia et America septentrionali" was fixed in that sense by Barabasch-Nikiforov (1947). Some authors consider Kamchatka as the type locality of the species (Ognev, 1931; Ellermann and Morrison-Scott, 1951, and others), which has little basis. To avoid undesirable nomenclature changes (renaming), the submitted interpretation of the restricted type locality must be sustained.

Steller's description of "Lutra marina" was given before 1758 (in 1751) and has no nomenclatral significance. "Viverra aterrina" of Pallas is sometimes submitted in lists of synonyms (Yakobi, 1938) but has no relation to the described species (Heptner, 1934). It is a kharza (see [Vol. II, pt. 1b]). In Erxleben, the name L. marina is associated with the given species only partially, because the author also had in mind the Brazilian otter.

Description³

Externally the sea otter is to the highest degree unique. Trunk elongated, of cylindrical form, and quite massive. Neck thickthicker than head, and short. Limbs very short, hind ones displaced posterior. Animal appears clumsy and heavy appearance. This impression is partially due to not only very luxuriant, although not very long fur, but also to skin loosely enveloping the trunk—as if in a sack. On land, movement of the animal is hesitating and relatively slow; while lying or moving, it usually flexes its back strongly. In water, it is very agile, mobile and flexible.

Head rounded, with dense long vibrissae and small eyes. Ear pinna small (resembles external ear of seals), auditory openings slit-like, may close (during submergence into water), nostrils are slit-like, closeable. The iris is blackish-tawny.

Foot flipper-like, all digits invested with common covering and fused to last phalanx; digit V (outer) very long, remaining gradually decrease in length to very shortest first; foot above and below covered with wool. Fore limb strongly shortened. Paw short, digits not segmented externally and only weakly defined. On lower side is found somewhat bulbous, round bare area, in anterior part of which four small parts marked by slight grooves corresponding to digits, and in posterior—one common narrow part extending transversely, [Fig. 328]. A second external part of fore limb includes two very long digits (on upper surface, there are correspondingly two claws), remaining one of three include one digit each. Claws of both fore and hind limbs very small, dark horn in color. Tail covered with a dense short fur, relatively short (about 25-30% of the body length), muscular and slightly flattened dorsoventrally.

Fur of sea otter not especially long, but exceptionally dense, soft and silky. It is one of the most precious furs, in fact is not comparable to any other fur as regards its beauty (especially "gray otter") and durability.

Guard hair and underfur differ little from each other in length, and are, moreover of more or less equal length throughout the whole body. The longest fur is in the middle of the back. In Commander otters, average length of guard hairs here is 27.7 mm,

³Mainly according to Barabash-Nikiforov (1947) and materials of Z[oological] M[useum of] M[oscow] U[niversity].

885



Fig. 327. Sea otter, or kalan, Enhydra lutris L. Sketch by A.N. Komarov.



Fig. 328. Lower surface of fore foot of kalan, Enhydra lutris L. Sketch by N.N. Kondakov.

of underfur-22.5 mm. For withers, 24.3 and 19.5 mm, respectively: for sacrum-24.5 and 21.7 mm. On scapula, hair length is 24.5 and 19.0 mm; on middle of side, 25.9 and 20.3 mm; on hip 20.3 and 16.4 mm. On breast, guard hairs have length of 25.3 mm; 886 underfur 15.0 mm; on belly, 23.4 and 17.0 mm; on groin, 21.1 and 15.0 mm. Maximum thickness of guard hairs is on breast (169.5 micron). On belly, it equals 147.6 [µ]; on middle of side, 136.6 $[\mu]$; on sacrum, 125.0 $[\mu]$; on middle of back, 123.9 $[\mu]$; and on hip, 115.3 [µ]. Tail is covered with shorter hair compared to trunk along its dorsum, length of guard hairs and underfur is 19.0 and 16.5 mm; along venter, 18.5 and 15.1 mm [respectively]. Guard hairs on dorsum of tail even coarser than on whole trunk (except breast): their thickness is 153.2 [µ]. On lower surface of tail, their thickness is 115.7 [μ] (all figures are mean of 50 hairs). On 10 mm² of back, an average of 12.4 (in summer), and 14.6 (in winter) guard hairs occur, as against 1910 and 1725 underfur hairs, respectively; on belly in summer, there are 20.2 and 1674, and in winter, 17.2 and 2221, respectively (Barabash-Nikiforov, 1947).

General color of fur is dark brown. Facial portion of head brownish-gray, light straw or almost white; vibrissae are white.



886 Fig. 329. Kalan on Mednyi Island, March 1964. Photograph by S.V. Marakov

Rear portion of head and occiput dark brown, sometimes mixed with separate white ("gray") and light reddish hairs (guard hairs with light tips). Fur on neck, withers and back dark brown, of an especially dense, deep, almost black, color on back. On the neck and withers, there is a significant mixture of yellowish-gray hairs, white and reddish guard hairs, and also on base of tail. Lower surface of neck and breast brownish-gray or even dirty-white. Abdomen dark brown, only a little lighter in tone than back. Transition in color from back to abdomen is gradual. Fore and hind legs similar in color to sides, but slightly darker. Gray hairs are absent on them. Upper side of tail same color as back and lower side—as in abdomen (prevailing type of Commander kalan, chiefly after Barabash-Nikiforov, 1947).

Individual variation in color is significant. General tone of fur, from the [above-]described and most widely-distributed type, proceeds through gradual gradations to deep pitch-black, or through



Fig. 330. Old kalan. Mednyi Island, May 1960. Photograph by S.V. Marakov.

tawny to light brownish. These differences are determined by characteristics of pigmentation of the terminal part of the hair—their bases have a very constant gray-straw color. Not rarely, there are significant exceptions to the described lightening of the anterior part of the trunk, and individuals are sometimes encountered with an almost white (cream-colored) head, neck (upper and lower) and breast. Otters with white heads and dark-sandy trunks belong to the category of extreme color deviants; completely white otters are also met with (albinos; Fig. 331).

Admixture of gray hairs is entirely variable. Usually, they are distributed on withers and anterior part of upper body, but sometimes occupy a greater expanse. Sometimes they are unevenly distributed, as in patches of different degrees of density. In a series of cases, they may be completely absent. Beside individual variation, the path and condition of molt itself have influence on degree of gray hair development (see below).

Seasonal changes in color and density of fur are insignificant. As in several other typical aquatic animals, molt in sea otters is not limited to a defined period, extending throughout the entire year, proceeding slowly, and pelage is always actually complete, or almost complete. However, molt is more intensive in summer months, which is responsible for noticeable differences between "summer" and "winter" fur. Before shedding, there is, in places, lightening of guard hairs, and therefore during the period of more intensive molt, the quantity of light (gray) guard hairs on the skin is greater. Therefore, intensity of molting, *i.e.* mainly summer animals, appear lighter—"gray". Except change in quantity of gray hair, which gives general fur color its tint, the basic color of the animal also changes somewhat. In summer, it acquires a lighter brown tone, apparently because of fading of the fur under the influence of the sun's rays (Reshetkin and Shidlovskaya, 1947).

Sexual differences in color are absent, or is only revealed in slightly lighter color of females. In females, the quantity of guard hairs is, on the whole, somewhat less, in connection with which their fur is generally somewhat softer.

Age variations in color are quite significant, and proceed slowly. Recently-born animals (*medvedoks*) have light brownish-red or reddish-tawny fur. Head and neck are lighter than remaining part of trunk, but the contrast is not as sharp as in adults. Abdomen is somewhat darker than back; fur is dense, but relatively short, with

888



Fig. 331. A group of kalans in Zapalat Bay on Mednyi Island. In the foreground—Albino kalan. On rocks, glaucous winged gulls (*Larus glaucescens* Naum.).

6 August 1962. Photograph by S.V. Marakov.

coarse guard hairs and is quite harsh to the touch. Such fur occurs in animals 5–6 months old or less. In a yearling, but not yet adult, otter (koshlaka), fur does not differ in color from that of adults, but, apparently, still contains some quantity of coarse guard pelage of the medvedoks. In both of these stages, gray hairs are absent. Maturity is attained by sea otters, apparently, in the fourth year. In young, the iris is nut-brown.

Geographic variations in color are poorly studied and, generally speaking, are insignificant.

Skull large and massive, high and broad, but short, with sharply shortened, high facial portion, as if vertically cut anteriorly [Fig. 332]. Its length is approximately two times less than cranial part of

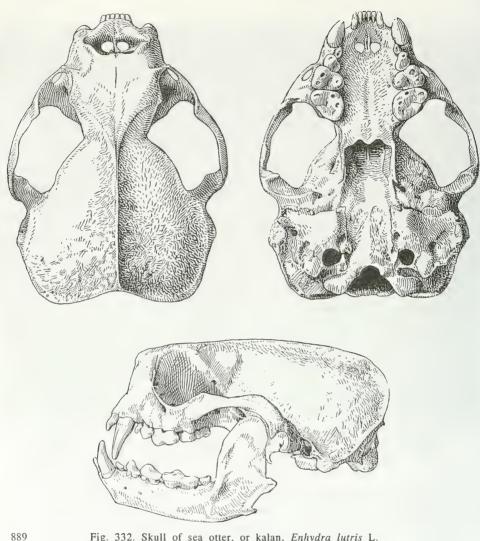


Fig. 332. Skull of sea otter, or kalan, Enhydra lutris L.

skull. Upper profile of skull almost horizontal, weakly rising posteriorly. Cranial portion of skull relatively very large and wide its width only slightly less than width of zygomatic arches. Zygomatic arches massive and strong widely separated laterally. Auditory bullae large, located transversely, auditory openings very small, directed obliquely upwards. Nasal bones short and broad. Upper processes of premaxillae narrow, extend to nasal bones, but 889 contact only their anterolateral processes. Postorbital processes

weakly developed. Postorbital constriction short and broad, constituting about one-fourth condylobasal length, but less than interorbital constriction.

Nasal openings terminate almost vertically, very wide—their width greater than width of orbit (from postorbital process to zygomatic arch). Nasal turbinates very strongly developed—intricately convoluted, filling the whole nasal opening and extending forwards nearly to its outer termination. Hard palate cleft behind cheek teeth very short and almost unconstricted. Sphenopalatine notch very short and wide. Diameter of infraorbital foramen is nearly equal to diameter of alveolus of upper canine. Mastoid processes isolated, blunt and massive, directed obliquely downwards. Opening of jugular foramen very large—its diameter approximately equal to diameter of alveolus upper canine or slightly less. Paroccipital processes very weakly developed. Coronoid process of lower mandible very large (60-80% of mandible length from angular 890 process to alveoli of incisors), angular process small. Protuberances and crests of skull on the whole, and sagittal occipital crests in particular, sharply expressed in old [individuals].

Dental formula—see the characteristics of the genus.

Individual variations in skull lie in several changes in general dimensions and proportional details. It is a fact, that not rarely there is in places asymmetry of the skull—somewhat stronger development of the left side of the braincase. This phenomenon is observed not only in old animals, where it is manifested in particular in twisting of the sagittal crest, but also in much younger animals.

Age changes in skull very great. In young, postorbital processes weakly developed, width of postorbital constriction less than width of interorbital area; facial portion of skull relatively still shorter; braincase, on the contrary, still more developed, more rounded and swollen; crests (sagittal and occipital) absent; suture between basioccipital and basisphenoid not fused*. In the upper toothrow, last tooth is third permanent premolar.

Sexual differences in skull not sharp, but obvious. Skull of female, beside smaller general dimensions, is distinguished by its relatively weakly developed crests, less massive zygomatic arches, narrower hard palate and some weaker teeth.

^{*}Russian word is zarosshii; lit. "grown over"-Sci. Ed.

Geographic variation of skull insignificant, manifested, apparently, only in general dimensions.

Os penis very large, quite massive and, on the whole, bent slightly upwards; anterior end forms slight bend towards ventral side. Usually, also small bend in lateral direction. At base, bone broadens and flattens, tapering anteriorly and becoming round in cross section. At extreme end, there is a small thickening with a deep depression on lower surface.

Body length of full adult (from four years old) and old individuals (Commander islands; 36), 100–136 cm (usually 120–130 cm); tail length, 30–36 cm; length of hind foot, 20–23 cm; length of ear, 24–26 mm. One especially large old *kalan* had a body length of 146 cm. Probably, in individual cases, body length may reach 150 cm (Ognev, 1931; Barabash-Nikiforov, 1947, 1962; Stroganov, 1962). Females somewhat smaller than males (accurate data absent).

Condylobasal length of male skull (31) is 124.2–145.9 mm, of females (9), 120.2–142.9 mm; zygomatic width of males is 96.9–116.2 mm, of females, 90.0–102.0 mm; interorbital width of males is 42.0–46.5 mm, of females, 36.7–42.2 mm; postorbital width of males is 28.0–36.0 mm, of females, 27.0–35.5 mm; length of upper toothrow (cheek teeth and canine) of males is 44.4–51.4 mm, of females, 44.3–49.2 mm (Ognev, 1931; Barabash-Nikiforov, 1947; materials of Z[oological] M[useum of] M[oscow] U[niversity]; Commander islands, a few specimens from Kamchatka).

New-borns have body length of about 38 cm (Brandt, 1880) and weight of about 1.5 kg; "not long after birth"—about 44 cm, tail length about 15.5 cm and weight about 2 kg; at two years old on average (36)—body length 80.6 cm, tail length 29.7 cm, and weight 19 kg; at 3 years old, on average (75)—body length 90.5 cm, tail length 31 cm and weight 21.2 kg; at 4–5 years old on average (17)—body length 101.5 cm, tail length 31.6 cm and weight 23.8 kg. Later, dimensions and weight gradually and slowly grow and the fully adult animal often weighs from 23.0–36.4 (37) kg. Males may attain weight of 40 kg, while weight of adult females is 20–25 (30) kg. With age, relative tail length decreases, constituting 35% of body length in recently-born animals; in 4–5-year-old animals—about 31%; and in 9-year-old and older—about 25% (Barabash-Nikiforov, 1947, 1962).

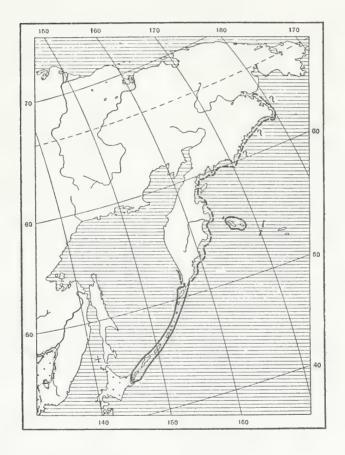
Os penis length 150 mm, width at base 15 mm (V.H.).

Systematic Position

Only species in the genus.

Geographic Distribution

Islands and in part shores of northern part of Pacific Ocean from approximately 62–64° N. lat. in the north, to Tropic of Cancer (in east [Pacific]) and 40° N. lat. on the south (in west [Pacific]).



891 Fig. 333. Range of the sea otter or kalan, Enhydra lutris L. in the USSR. Solid line—present range; broken line—reconstructed. Cross designates local settlement on Moneron Island. V.G. Heptner.

Geographic Range in the Soviet Union (reconstructed mainly according to materials of Snou, 1902; Tikhenko, 1914; Barabash-Nikiforov, 1947; Uspenskii, 1955; Gribkov, 1963).

This occupied the southern coast of Sakhalin (apparently, Aniv Bay and somewhat to the north of Cape Aniv along the Okhotsk coast)* and the whole Kuril chain from the southernmost islands (Shikotan and Kunashir) to Shumshu and Atlasov.

In Kamchatka, along its western (Okhotsk) coast, sea otters even in the 18th century, apparently, were present only in the extreme south and did not extend north beyond the mouth of the Igdyg River (Ozernaya) and the Kambal' and Kitov capes (Steller, 1753, mentioned that in the "Penzhin River" sea otters were absent). In any event, they did not live in Shelekhov Gulf, or perhaps only very rarely intruded there (Steller's data, given below, concern only the eastern shore of the peninsula). Frozen sea and fast shore ice excluded their existence.

Along the eastern shore of Kamchatka in the "Otter Sea", in the first half of the 18th c[entury], kalans were distributed between 50° and 56° N. lat. chiefly from Cape Lopatka to the Kronotsk Peninsula (Steller, 1753), more precisely, to Cape Stolbov (a little north of the latitude of Bering Island—about 56° N. lat.). According to less definite information, in the past (18th and first half of 19th c[entury]) they extended northward to 60° N. lat. *i.e.* approximately to Olyutor Bay and even to Cape Faddey and the mouth of the Anadyr' [river], in other words, approximately to 64° N. lat. However, information concerning its occurrence at 60° N. lat.** and more to the north, is doubtful, or related to occasional transgressions of drifting.

A separate section of occurrence, not connected with the mainland portion of the range is found in the Commander islands, situated at approximately 180 km in the open sea from the nearest part of the Kamchatka coast. It is also isolated from the other part of the range which occupies the Aleutian islands—about 350 km from Attu Island.

During the 18th, and especially the first half of the 19th c[entury], there was very intensive, entirely unregulated hunting of the animal throughout the whole range within, as well as outside, the boundaries of the USSR. The highly prized fur of the sea otter

892

^{*}Not shown on map, Fig. 333-Sci. Ed.

^{**}Contradictory-Sci. Ed.

was, as is known, one of the main stimuli for taking possession of the northern coast of the Pacific Ocean, at first, by individual Russian explorers and later by the "Russian-American Company". In the second half of the 19th c[entury], after the Company ceased its activities, and in some places much earlier, the animal was practically exterminated in the greatest part of its region of occurrence in our country. It completely disappeared from the continental coasts and Kamchatka, except Cape Lopatka. On the eastern coast of Kamchatka, in Kronotsk Bay, the last time *kalans* were, observed, apparently, was in 1852 (Ditmar, 1901).

At the beginning of our [20th] century (up to 1943), otters temporarily disappeared completely, apparently, from Lopatka, or their number decreased so greatly that information of their existence there was questionable. However, in 1943, there were about 300 individuals (Averin, 1948); they are there now at the present time (beginning of the 60's).

On the Commander islands, as a result of the senseless harvest in the 18th c[entury], it is considered (Marakov, 1964) that kalans were completely exterminated and were absent here for about 100 vears—until the 70's of the 19th clenturyl, when they were observed again. It is supposed that they resettled on the Commander islands across the sea. This is, however, quite doubtful. At least the present situation of populations of Mednyi and Bering islands points to the settled mode of life of the Commander kalans and to the low probability of their surmounting the large expanse of open ocean. On the first island, the otters are numerous and on the second they occur individually, although the islands are separated by a strait whose width is all of 24 km. Therefore, it is more probable that a very small number of animals was preserved from extinction on the islands and they, under conditions of complete prohibition of their pursuit, had the possibility of reproducing again. In any event, at the beginning of our [20th] century, there were already about 400 (Suvorov, 1912). Afterwards, they were mainly preserved because in this place, long before the Revolution, the state hunting of sea otters and fur seals was organized. On Mednyi Island, animals were always more numerous than on Bering Island.

Otters had already disappeared from southern Sakhalin very long ago, and at the present time are absent there. On the Kuril islands, otters were from time immemorial, as is said, always present everywhere. However, pursued both by Russian and also many

foreign fur companies in the 19th c[entury], otters quickly decreased in number and their distribution was reduced. Their numbers continued to decrease in the 20th c[entury]. On the brink for two centuries, in part at the beginning of our century, they, although rare, occur on a quite considerable number of islands—Shumshu, Paramushir, Onekotan, Kharumkotan, Ekarma, Matsuva, Raseva, Ketap, Chirpo and Kunashir (Tikhenev, 1914; Uspenskii, 1955). On the other hand, in 1912, some authors believed that otters on the Kuril islands disappeared almost completely (Suvorov, 1912). Information concerning the 30's (Barabash-Nikiforov, 1947), actually points to the complete absence of otters in the archipelago, except for a few in Shumshu and between Onekotan and Urup.

Difficulty of access to many parts of the archipelago, especially the small islands of its middle part, permitted the animals, at least in very small numbers, to protect themselves until the 40's of our century. In the very first post-war years it was established that sea otters inhabited Paramushir, Onekotan, Shiashkotan, the Musiru, and probably several other small islands of the middle part of the chain (Solov'ev, 1945; Sergeev, 1947; Kuznetsov, 1949).

By the middle of the 50's and the beginning of the 60's, *i.e.*, within 10–15 years of initiating protection, the number of kalans in the Kuril islands grew strongly and their range broadened; the cause of this may be only partially correlated, owing to better censusing and inspection. In 1955, the population of Kuril *kalans* was in any event not less than 1500 individuals, and they lived on Paramushir, Antsiferov Island (Shirink), Onekotan, Shiashkotan, Rasshua, Simushir and Urup. South of Urup, animals were not recorded (Klumov, 1957). After 1955, growth of the Kuril sea otter population and the expansion of their range continued, and in the mid-60's, they occupied the whole archipelago, were more common south towards Urup (B.G. Voronov), and especially common on Urup.

At the southern extremity of Kamchatka, sea otters were distributed (information from the 40's and 1960) not only at Cape Lopatka; along the Okhotsk side, they lived to capes Kambal' and Kitov, along the ocean north to at least Gavryushin Kamen' Island (Cape Il'ya, Cape Zheltyi, Cape Inkanyushin, Utashud Island, Gavryushin Kamen' Island; Barabash-Nikiforov, 1947; Gribkov, 1963). All these places are located in southernmost Kamchatka, south of 52° N. lat. and are associated with Cape Lopatka. Kalans

have now spread, however, and are considerably more to the north. Thus, in 1960, one animal was found in the delta of the Avacha river in Avachin Bay, and another (in winter) at the former Ust' Kamchatka region at 57° N. lat. *i.e.* north of this place, which Steller (1753) referred to as the [range] limit. The latter animal was caught in the river 20 km distance from the sea shore (Gribkov, 1963).

At the end of the 50's, kalans were introduced to Moneron Island, lying approximately 50 km west of the southwestern end of Sakhalin. The animals at first survived, but later died (G.V. Voronov).

Therefore, the present range of the kalan occupies the Commander islands, the extreme southern end of Kamchatka (Cape Lopatka and adjacent places) and all the Kuril islands. The rough number of animals apparently exceeds 4000 individuals.

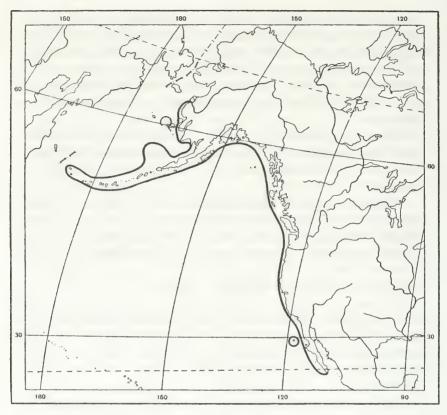
Geographic Range outside the Soviet Union

Along the Asiatic coast, kalans were encountered on the coast of Hokkaido (Yeso), apparently, northern, eastern and southern and at the northern end of Honshu (Hondo, Nippon). These may in part be wandering animals (Temminck, 1847; reference to northern shore of islands).

In the eastern part of the Pacific Ocean, sea otters were present along the entire Aleutian Island chain, in the Pribilof islands and along the American coast and adjacent islands from approximately 60° N. lat. (almost from the mouth of the Yukon—at least along the shore of the Alaska Peninsula) southwards to the middle part of the California Peninsula [Baja California] (Sebastian Vizcaino Bay at Cedros Island, about the latitude 28° N. lat.; Hall and Kelson, 1959) and, perhaps, even Guadalupe Island. There is information on their occurrence to the southern extremity of [Baja] California, *i.e.* to the Tropic of Cancer.

In the beginning of our century, in all American sections of the range, kalans were destroyed almost everywhere and were met with in very small numbers only along the Aleutian chain and perhaps individually in the San Francisco region* and in other separate places. In San Francisco, where sea otters were considered to already have been extirpated long ago, they unexpectedly

^{*}Actually, Monterrey and Big Sur, south of San Francisco Bay-Sci. Ed.



894 Fig. 334. Reconstructed range of the sea otter, or kalan, Enhydra lutris L. on the coast of North America. V.G. Heptner.

appeared in the 30's in quite considerable numbers (Bolin, 1938; Fisher, 1939). Thanks to their protection, the population of otters in America quickly grew; at the beginning of the 60's they were already quite significant. Consequently, their range has also widened. The question now concerns organizing utilization of the animals (V.H.).

Geographic Variation

Geographic variation in the kalan is poorly understood. Collection materials of skins in museums are very few because of their very high price, and these skins are often old and their color has changed.

894 Conceptions of species variability are, therefore, based mainly on craniological features and only partially on color and fur characters.

Within the USSR, two races may be distinguished⁴.

1. Commander sea otter, or kalan. E. l. lutris Linnaeus, 1758 (syn. marina).

Fur color relatively light, with significant development of gray hair and quite long guard hairs (30 mm long on the average, in middle of back). Skull fairly large, moderately wide. Zygomatic width constitutes 71–80% and mastoid, 71–79% of condylobasal length.

Condylobasal length of skull of males (17) is 130.5–M 136.5–140.3 mm, of females (7), 120.0–M125.4–128.2 mm; zygomatic width of males is 101.0–M 104.3–110.0 mm, of females, 90.0–M 94.3–102.0 mm; interorbital width of males is 40.2–M 43.4–46.5 mm, of females, 36.7–M 39.2–42.2 mm; mastoid width of males is 93.9–M 99.5–108.0 mm, of females, 88.0, M 91.4–95.3 mm; length of upper toothrow in males is 46.2–M 48.3–51.4 mm, of females, 44.3, M 46.0–48.6 mm.

695 Greatest skull length is 144.2 mm on average (Barabash-Nikiforov, 1947).

Commander Islands.

Outside the USSR, Aleutian and Pribilof islands, and on the American coast, from the northernmost place of occurrence south to Vancouver Island inclusive.

2. Kuril otter, or kalan. E. l. gracilis Bechstein, 1799 (syn. crientalis, stelleri, kamtschatica).

Fur relatively dark, with weakly-developed gray hair and a relatively short guard hairs (on middle of back, about 25 mm long on average).

Skull somewhat smaller, wider than in nominal form and somewhat flattened. Zygomatic width constitutes 85–87%, mastoid—84–86% of condylobasal length.

Condylobasal length of skull (5 old males; Kamchatka) is 132.8-M 133.4-133.6 mm; zygomatic width is 113.3-M 114.9-116.4 mm; interorbital width is 46.9-M 48.0-49.1 mm; mastoid

'Characteristics of the races after Barabash-Nikiforov, 1947 and Stroganov, 1962. Description of fur of different races by Barabash-Nikiforov, 1947 is, however, slightly contradictory. In contrast to other authors, he indicates (p. 26) a "tawny sheen" on fur of Kamchatka animals, giving fur even a "reddish" color, compared to fur of Commander animals. On the other hand, he refers to a "darker tawny tint" of fur of Kamchatka animals. The review of Stroganov (1962) does not give anything new and only complicates the picture (it refers to the existence of "not less than five" races of the species). From this work, if not with reservations, data on dimensions and proportions are taken.

width is 107.0-M 109.5-112.3 mm; the length of upper toothrow is 46.2-M 46.6-47.0 mm.

Greatest length of skull is 137.3 mm on average (Barabash-Nikiforov, 1947).

Kuril islands, Kamchatka, and in the past, in South Sakhalin. Outside the USSR—in the past, northern Japan (Hokkaido, and possibly northern Honshu).

The attempt to separate Kuril and Kamchatka sea otters into separate races (Stroganov, 1962), must not be considered justified. Those geographical considerations on which this was based do not give any basis for this. There is no isolation between kalans inhabiting different parts of the chain; nor is the Kamchatka population isolated from the Kuril. Sea otters not only drift with currents and storms (to which even Steller, 1753 referred), but they themselves undertake quite large migrations and undoubtedly move from one island to another. Apparently, the populations of Cape Lopatka and Shumshu Island communicate with each other⁵. In particular, this is inferred from information given above concerning the "disappearance" and "restoration" of the Lopatka population during the last ten years. It is also known that in the pre-war years, Japanese kalan hunters tried more than once to "drive" Lopatka animals to Shumshu using various means.

Kuril kalans were once considered the very best and were especially valuable. Kamchatka were also esteemed more highly than Commander [otters]. This correlation of values corresponds to racial difference between Kuril-Kamchatka and Commander [otters] and to a certain degree, indicates the isolation of the Commander population.

Outside our country, only one well distinguished form is apparently known: *E. l. nereis* Merriam, 1904—the North American coast south of Vancouver Island (V.H.).

Biology

Population. In the second half of the 18th century, populations of kalans were still significant in some places. Concerning this one may judge from the fact that on the Pribilof islands, in 1787, more than 5000 kalans were caught. Later, their number greatly decreased,

⁵Width of the First Kuril Strait, separating them "reaches 10 miles, but free passage is reduced to 3.0–3.5 miles due to reefs present on both shores" (Sergeev, 1947).

from killing and in 1821 the harvest was prohibited, and by the 896 40's they completely disappeared here. During 1763-1764 on the Andreyanov islands, about 3000 kalans were taken, and during 1775-1780, on Urup (Kuril islands)—1170. After the strong earthquake of 1780 kalans disappeared here. With renewal of harvesting on the Kuril islands, during 1828-1830, 2600 animals were caught on only Urup and Simushir. For 1842-1860 on the Kuril islands, 4510 individuals were taken overall, i.e. an average of only 250 animals per year. In 1745, on Bering Island more than 1500 kalans were captured, and from 1747-1749, an additional 1500. As a result, for the period 1754-1755, a total of 5 kalans were caught, and in 1756—not one. In 1762, 20 head were taken and after that, the harvest was suspended for a long time in view of the trifling results—kalans were very few. Therefore, on Bering Island during the second half of the 18th century, the stock of kalans was slightly more than 3000 head. With depletion of the otter stock on Bering Island, the main harvest was shifted to Mednyi Island. Here, in 1754, no less than 790 otters were caught, and during 1760-1763, no more than 20. Here, probably, the population was half that on Bering Island. Overall, apparently, only 4000-5000 of these animals inhabited the Commander islands, since there is information that the quantity of kalans on Mednyi Island attained 2000. From these uncoordinated figures (complete data for whole range are absent), the conclusion may be drawn, that at the beginning of the 18th century, the kalan population consisted of approximately 20-30 thousand (possibly slightly more) in the whole range—from the northern coasts of Japan to the shores of [Baja] California. In the latter area, during the past century, 7000

In order not to undermine the basic stock, not more than 2000–3000 animals could be harvested every year throughout the whole range. In the period beginning in 1870, the world take of kalans fluctuated within the range of 4000 to 8000 head, on average 5000 head per year. Therefore, the entire time harvest was always at the partial expense of the basic stock, and the result was that after the harvest of 8000 head in 1884, it steadily decreased; in 1900, it was reduced to 1000 head. This decrease continued until the nearly complete liquidation of legal harvest in the beginning of this century. Within more than two centuries, otters were almost destroyed due to their rapacious exploitation.

skins were bought from the native hunters in only one year.

On the Commander islands, after the period of almost complete disappearance of kalans, they appeared again in the 70's of the previous century, but only on Mednyi. The main stock of Mednyi Island settled mostly on the northern (northwestern) extremity of the island. Disturbed by a take of living animals in 1937–1938, the herd migrated to the southeastern extremity (Il'ina, 1950). Ten years later, kalans returned again to the northern extremity of the island. If in 1931–1932, 282 kalans were counted in the waters of Mednyi Island, then in 1952, 250 animals were recorded (O. Danilov), and in 1955 about 350 (Marakov, 1964). Therefore, despite the absence of harvesting due to some reason which were difficult to eliminate, the Commander stock of kalans hardly grew during the last 20 years.

In 1924, on both Commander Islands, 400 individuals were counted; in 1939—800; and in 1957—500 (Nikolaev, 1958). During the last decades, the situation sharply changed, and the kalan population began to grow quickly—in 1964, on Mednyi, the number of adult animals alone reached 1000 (Marakov, 1964). As shown above, the population of sea otters on Bering is very small; they



Fig. 335. Habitat of kalan on Mednyi Island. Photograph by S.V. Marakov.

are encountered individually. It follows that growth in the number of animals is correlated to their reproduction locally—the possibility of their immigration from outside is, in practice, very improbable (Marakov, 1964). It must be noted that recent methods of counting still allow significant discrepancies between data of various authors. Thus, in 1931, according the Commander state fur farm put the number at 282, but from another source of data (Barabash-Nikiforov, 1948)—about 500.

Kalans of the Kuril chain and Kamchatka constitute one population, which is characterized by regular seasonal migrations (Dobrovol'skii, 1936; Nikolaev, 1958). In the Kuril chain, there were 200 in 1912; in 1924-600, and in 1939-800 kalans. By autumn of 1958, north of Iturup there occurred about 1900-2200 animals living; and by 1961, the population increased to 2900-3100 head. On the islands of the archipelago inhabited by kalans, they were most numerous on Urup-938 animals in 1958, and 1700—in 1961, and on Paramushir where in 1958, 614 individuals were recorded. In the remaining cases, the number of recorded animals did not exceed 79 (1958). Relatively more animals were observed in the waters of Shikotan, Ketov and Simushir islands (Nikolaev, 1958, 1964). On Kamchatka in 1910, about 306 sea otters were censused, in 1924-400, and in 1943-again only 300 (Averin, 1948). The total number of our kalans at the beginning of the 60's, apparently, exceeded 4000.

On the islands of the Aleutian chain and the shores of the Alaska Peninsula in 1912, there were about 200 otters; in 1924—200–250; in 1958, thanks to rapid growth of the population, the number had already reached several thousand. In the waters of the California coast (36° parallel and south), in 1938 in all 94 were censused; but in 1958, already there were about 500. According to the most recent data, along the coast of the state of Alaska there are 20–30 thousand otters. It is calculated that on the islands of the Aleutian chain, in particular on the Rat, islands, the kalan population has already reached its density limit (Kenyon, 1961). In 1962, with examination of six main sections of occurrence from the air, 11000 kalans were counted (Brooks, 1963). Attempts to settle these animals on the Pribilof island have still not succeeded.

Proceeding from the given data on America and paying attention to information on the animal's population in the USSR and in California, the total number of kalans may be determined as



898 Fig. 336. Biotope of kalan. Babichii Pod'em Bay on Mednyi Island. Photograph by S.V. Marakov.

25–35 thousand head. Apparently, this species' extinction, anticipated not long ago, no longer threatens it. Protection of the sea otter is one of most remarkable in the field of nature protection.

Habitat. Habitat of the kalan is characterized by steep rocky shores, barrier reefs, submerged and exposed rocks, continually washed over by waves, as well as vast thickets of sea weed (species of Alaria and Laminaria—"sea cabbage") extending as an interrupted belt along the shore. The latter grow strongly in summer, but are destroyed by storms in winter. Everywhere where they exist at the present time, kalans prefer the extremities of islands and peninsulas. Here the animals have the possibility of moving around to the lee side in stormy weather.

Condition of the water medium, feeding and climate are in total more important for kalans than the character of the coastal belt itself. Their inclination toward inaccessible coastal zones de-

veloped as a result of savage pursuit. In structure and type of adaptation, the animal is not only littoral but also pelagic, adapted to living under conditions of the northern part of the Pacific Ocean. This is a marine climate, with mild winter and cool summer, and fog, frequent drizzle and entirely variable, but occasionally severe, winds especially in winter. These winds, and especially storms, are very unfavorable for kalans. The small difference between air temperature and that of the upper layer of water seems to be a positive factor, especially in summer. The difference in water temperature during a year on the Commander islands is only 15°C in all (from-1.5°C in January to 13°C in August). In the Kuril chain, water temperature fluctuates from—1.8°C in January to 5-10°C in the northern islands and 10-20°C in the southern islands. The lag of the period of greatest coolness at a depth of 20 m and more, has large significant in the ecology of marine animals serving as food for kalans. During experiments on acclimatization on the Murmansk coast (Reshotkin and Shidlovskaya, 1947), kalans suffered some from summer heat and mosquitoes.

Food. On Mednyi island, two species of sea urchin serve as the main food of kalans; bivalve mollusks are of significant importance—octopuses are less so. In numbers, crabs of several species constitute 10%, but fishes—6.7%, of which cod, lumpfish [Cyclopterus lumpus], Pacific capelin, sand eels [Ammodytes] and sockey salmon predominate. Altogether, 28 food components were established. When held in captivity, the kalan reveals great frugality in feeding. Under natural conditions, its food regime is fairly monotonous (Barabash-Nikiforov, 1947).

The chief characteristics of the animal's nutrition in the autumn-winter period on the Commander islands consist of the fact that at this time there is a sharp fall in the proportion of crabs (from 24 to 4%) and fish (from 22 to 6%) which migrate at that time from the shores into great depths of water. The proportion of mollusks slightly decreases, from 50 to 45%. Sea urchins remain the main food component (100–98%). On the Pribilof islands, sea urchins also constitute 92% of the kalan's food (Murie, 1940). This is also confirmed by observations on otters in nature, on Mednyi Island (Barabash-Nikiforov, 1947). On Urup (Kuril chain), in February-March, kalans in the western (Okhotsk) coast feed on sea urchins, polyplacophore, gastropod and cephalopod mollusks, crustaceans, starfish, fish and algae. Along the eastern coast at this



Fig. 337. Zapalata Bay on Mednyi Island—place of residence of kalans. Photograph by S.V. Marakov.

time, crustaceans occupy first place, various mollusks—second, and then—sea urchins and algae (Nikolaev, 1958).

In captivity, the daily [dietary] norm of the kalan constitutes 4.5–5.5 thousand calories (Reshotkin and Shidlovskaya, 1947). According to other data, for the average sea otter, it is 6.5–7.5 thousand calories, but for large animals—even 10 thousand (Il'ina, 1950). Proceeding from the fact that the quantity of sea urchins eaten by a kalan in one day contains only a total 3 thousand large calories, some (Il'ina, 1950) consider that, in freedom, fish must predominate in the kalan's food, and kalans cannot feed on sea urchins alone. In captivity, food of the kalan consisted of fish (66.8%) and sea urchins (33.1%). As concerns digestibility, the fish proportion increases to 80.3%, and sea urchins drops to 19.6% (Il'ina, 1950). It is impossible to consider that the question of kalan nutrition has been sufficiently clarified.

Home range. Kalans do not reveal an attachment to any sort of definite place. Individual animals and groups of them appear irregularly in first one place and then another; however, true



Fig. 338. One of the groups of kalan of Mednyi Island. Photograph by S.V. Marakov.

migrations are only observed in separate individuals and pairs. Periodic redistribution of the kalan populations in the region of their permanent habitat which happens locally, depends first of all 900 on the weather. With a wind of velocity 4, several concentrations of them are observed at the shore. This becomes very obvious with wind velocity 7. In calm summer weather, separate kalan groups stay permanently at a distance of 18 and more kilometers from shore, where there are shallow places (banks), with beds of sea cabbage [kelp]. Here they spend the night. In winter, kalans gather themselves at the shores, since the kelp beds are destroyed by storms. In the open sea, kalans may be met with at a distance of 18-27 km from shore, but they are capable of reaching considerably greater distances. The appearance of killer whales* (which usually cause otters to flee in panic), human activity and the exhaustion of main foods, are reasons for local regrouping of kalans; such was the case in 1938, when on Mednyi Island sea urchins almost completely died out following some sort of epizootic (Barabash-Nikiforov, 1947).

^{*}Russian name is "kosatka", misspelled "kasatka", or swallow, in Russian original—Sci. Ed.

Among kalans of the Kuril chain are distinguished local ones which are permanently present in one and the same place as migrating ones.

In summer, kalans here completely confine themselves in definite sections of the shore, although they sometimes move for tens of kilometers in search of food and protection from storms.

Burrows and shelters. For resting, kalans utilize sections of rocky laida, narrow coastal strips under steep coastal cliffs, especially in times of winter storms. For the same purpose, they very frequently use the emergent and submerged rocks ("hiding-places*") at various distances from the shore. In summer, otters also frequently use dense kelp beds, which are sometimes considerably far away from the shore, for resting and protection from the attack of killer whales.

Daily activity and behavior. The kalan is an animal preferably active during the day. Its activity begins at dawn or shortly before it, and ends at twilight. At night, the kalan is active only on rare occasions, usually on moonlit nights. In winter time, the animals spend the night on shore and eat the entire day without an interval



Fig. 339. Kalan lying in water, May 1960. Photograph by S.V. Marakov.

^{*}Russian word is tainiki-Sci. Ed.

in the activity for resting. In summer, they feed mainly in morning and evening, resting from 11–12 to 15–16 o'clock. In this time, the animals stay in the algae beds, gathering in herds of 20–120 head. Old otters, sometimes "twist", wrapping themselves in algae and appearing as if anchored (Fisher, 1939).

The degree of activity of the kalan depends upon the provisioning of the given region with food, the weather conditions and the state of the sex glands. Animals are more active in regions with small food supply. Males also manifest increased activity in search of females in estrus. Before storms, activity of kalans also grows in connection with relocation to protected places. The kalan feeds several times in the course of a day. After satiation, it cleans itself, sometimes plays, and then rests in the water, lying on its back. In the open sea near shore, the kalan may feed even with wind strength of 6–7.

In the sea, the sea otter is agile, mobile and quite quick. In searching for food, it moves at a speed of 5-6 km/h, but its maximum speed equals 12-16 km/h (A.M. Nikolaev). Capture of



902 Fig. 340. A group of resting otters on the rocks of Glinka Bay, Mednyi Island,
December 1958. Photograph by S.V. Marakov.

bottom and swimming fish is with its teeth and fore paws, then clasping them to its chest. Coming to the surface, the animal lies on its back with it and in such a position eats it. This pose is very characteristic for the animal in feeding and resting. After taking food, the kalan cleans itself of the remains by revolving around on its [body] axis. After resting, kalans often gambol, play with each other and somersault in the water. The kalan is a herd animal, and peaceful for the most part with respect to each other. However, fights between males for females occur in places. On land, kalans move quite slowly, strongly bending their back while walking, like the river otter. Droppings on land with abundant remains of sea urchin tests and remains of crabs, mollusks and fish serve as a characteristic feature of the kalan's residence.

Seasonal migrations and transgressions. Until recent times, it was considered that kalans do not perform significant and regular migrations. This idea was based on observations of herds of the Commander islands. In actuality, a significant part of the Kuril 902 (perhaps Kuril-Kamchatka) population gradually translocate themselves from wintering places on Iturup and Urup islands northward to a place of spring residence on the middle islands of the chain— Brouton, Onekotan—where the animals spend March and April. Then they move farther to summer (May-October) on the northern islands-Paramushir, Shumigu, Aland and perhaps to the Kamchatka coast.

In autumn, a local reverse migration to the south takes place. Autumn migration of kalans from the northern islands of the chain is associated with decrease in water temperature toward -1.8°C, which causes displacement of the bottom fauna to deeper places, complicating food capture. Another cause leads us to think it is the appearance of ice which hinders movement and food-catching. At the end of January, cooling of water to -1.8°C and the appearance of ice drive the kalans away from the shores of Iturup Island and in March, also from the Urup coast. The coastal waters of the middle islands remain free from ice in March-April.

In the time of migration, kalans swim singly and in pairs at intervals of 10-15 min[utes]. During migration, all animals securely hold to a definite direction, neither stopping nor paying attention to local kalans. Nevertheless cases occur of single individuals (possibly young) who lose their way and return (Nikolaev, 1958).

In addition to seasonal migrations which do not include the entire kalan population, more than once there was observed translocation of a herd for a considerable distance, after which the animals reappeared in the abandoned places, sometimes only after a series of years. Such was the case when kalans disappeared from Urup after the earthquake in 1780, and also a series of cases when the disappearance of kalans in one region was accompanied by sudden growth in the population of another. In the 40's of the previous century, otters disappeared from the shores of Simushir Island after the eruption of Prevo volcano. At the same time, they appeared on Shumshu, Rasshua and Ushishir islands, where they absent earlier. Kalans temporarily left Cape Lopatka after the wreck



Fig. 341. Females with young and pregnant female otters. Mednyi Island, Zapalata Bay. 6 August 1962. Photograph by S.V. Marakov.

of a Japanese ship. Finally, it is sometimes believed possible (Barabash-Nikiforov, 1947), to connect the secondary appearance of sea otters in the 70's of the last century on the Commander islands (after their complete or almost complete destruction there by the end of the 18th century) with increase of the harvest at that time on the Aleutian and Kuril islands, which might have caused their resettling on the Commander islands. As shown above, this idea is lacking in foundation. There is the suggestion that all kalan populations, with the possible exception of the isolated California group, constitute one chain, within the boundaries of which displacements and regrouping can, apparently, occur.

Reproduction. The kalan, apparently, attains sexual maturity in the third year of life, but this is not accurately established. The kalan has no definite estrus (rut) period. Nuptial games, mating and new-born young with the females are observed at any time of the year. On Mednyi Island, nuptial play was somewhat more often observed in spring—March—May, but it was also observed in July—August. On the Kuril islands, the mass parturition proceeds in spring, but new-borns are also observed at other times of year (Nikolaev, 1958).



Fig. 342. Female kalan with the new born on its chest. Mednyi Island. Photograph by S.V. Marakov.

The duration of pregnancy is determined as 8–9 months; in one case, it lasted 238 days. The female, as a rule, bears one cub.

904 In very rare cases, two embryos were found; still rare—two cubs with a female.

Mating takes place in water and lasts 3–9 min[utes]—parturition—on the shore or on rocks flooded with water. Delivery lasts about two hours. In several cases, the cub of the previous litter, already almost equal to her in dimensions, is still with the parturating female. Clearly-defined [mated] pairs are absent among otters.

The annual increase of the kalan population on Mednyi Island was determined in the 20's-30's of the present century as 7% or less (Barabash-Nikiforov, 1947). These figures characterize the tempo of growth of a herd strongly undermined by predatory harvest. Rate of annual growth may be judged by the percent of yearlings in the population. According to data of the autumn count of 1958, on Paramushir, the growth was 10.5%, Onekotan—6.6%, Shiashkotan—14.0%, on Ketoi and Simushir islands—8.5%, Urup—7.8%. Therefore, the probable annual growth of the Kuril



Fig. 343. Otters going to water. Mednyi Island. May 1958. Photograph by S.V. Marakov.

population fluctuates within limits of 6.6 to 14.0% (A.M. Nikolaev). Average equaled 9.2%, which is somewhat higher than earlier figures given. It is undoubted, that in the thriving period of the species, natural increase is higher—within limits of 10 to 20–25%.

Growth, development and molt. Immediately after birth, body length of new-born is 50–56 cm, and weight, 1.4–1.6 kg. Kalans are born able to see, with juvenile fur and having 26 milk teeth. In the first days after birth, they are barely active, and lie on their backs on the shore or in water. First attempts to swim independently are made at the age of about 2 1/2 weeks, and by the third week, they are already able to swim for short distances. The juvenile (infant) fur is replaced by permanent at the age of about 6–7 months. At this time, replacement of milk incisors and first premolars by permanent is completed. Replacement of second and third premolars begins, and the molar teeth erupt. Total number of teeth is already 32. Body weight of such a "koshlak" reaches 9–11 kg, body length, 1.10–1.15 m. At one year, live weight reaches 17–19 kg and body length, 1.25–1.35 m. Replacement of premolar teeth is completed, but skull crests are still weakly developed (II'ina, 1950).

Enemies, diseases, parasites, mortality, competitors, and Dynamics of number. Among animals, the most dangerous and almost the sole enemy of kalans is the killer whale which often manifests itself in otter habitats. The polar shark is rare and is mainly found at great depths. Old information, that Steller's sea-lions and fur seals also appear to be enemies of the sea otter, have not been confirmed by more recent observations. The largha seal is a competitor of the kalan as regards main food components, and in respect to shelters, Steller's sea-lions, fur-seals and other pinnipeds are competitors. Several of the sea birds are shown to be competitors, in small degree of the kalan. However, their activity has no fundamental effect on food resources of the kalan. Natural mortality of kalans is very great. Causes show up as age limits, diseases. injuries caused by killer whales and, possibly, sharks; rockfalls on to shore laidas; the breaking of ice (Nikolaev, 1958), and in individual cases, the effect of storms and birth pathologies. Age limit of the kalan is not known. Judging by the relationship between the intensity of reproduction, animal dimensions and duration of life, in kalans it must be considerable.

There are no reliable data concerning population dynamics of otters. For the last 200 years, the human role was so great that other factors were overwhelmed and could not be estimated.

Besides direct destruction, the movement of ships in the region of their habitat and frequent frights caused by other human activities have an extremely negative effect on the numbers and of kalans and their colonies on the coastal belt.

Practical Significance

The economic significance of the kalan is very substantial. This now rare animal provides beautiful, warm and durable fur and is considered the most valuable fur-bearing animal. Individual otter hides have been sold at the London auction for a price of \$2000. The value of the fur is doubled by the rarity of the animal: for the past 80–100 years, not more than 8000 hides were sold per year, and in the past 30 years—a negligible quantity (single ones), and more or less accidentally.

In the USSR, the harvest was prohibited in 1924. This prohibition continues until the present with the aim of future growth and dispersal of herds. Because of the low reproductive rate of kalan and conditions not yet entirely favorable for them; at the present time, conditions for restoration of initial population require sufficiently more time. At the present time, the question has been raised concerning a possible catch of a limited number of otters, especially the sick and old, for skins (in nature, mortality in this species is relatively very high: Marakov, 1964). Along the American coast, where the density of otter colonies locally has already reached its limit, a test harvest was conducted in 1962 and 174 animals were caught (Amchitka Island); in the following year, there was planned a harvest of up to 300 individuals for determining the possible price in the fur market (Brooks, 1963).

Several perspectives may be borne in mind concerning cage rearing of otters; experiments to keep them in captivity have been relatively successful. However, feeding the animals on their natural food in captivity is very complicated, since preparation of this food which is needed in large quantities for each animal is difficult. The experiment of the keeping animals in open-air confinement on the Murmansk coast of the Barents Sea, may be also considered partially successful.

The main means of catching otters in the shutter net, and in summer, the landing-net. At the epoch of abundance of this animal, harvesters caught it on land by hitting it on the head with a stick (P.Yu.).

906

Superfamily of Wolves

Superfamilia Canoidea Simpson, 1931

Family of Raccoons

Familia Procyonidae Bonaparte, 1850

Predators of small, moderate and large dimensions, in part generalized, and in part specialized and highly specialized types¹.

Limbs are pentadactyl, plantigrade and semi-plantigrade; digits separated to different degrees, the third—longest; claws in majority of cases non-retractile, in a few, semi-retractile (*Ailurus*, panda; *Bassariscus*, cacomistle). The lower surface of foot and hand usually bare.

General form of skull variable—in some species facial region elongated, in others, skull short and rounded; in still others, whole skull strongly elongated. However, in the majority, braincase relatively, sometimes very, voluminous. In majority of species, alisphenoid canal is not developed, canal of carotid artery (can. caroticus) located at inner side of auditory bulla and separated from posterior lacerate foramen (for. lacerum posterius).

Dental formula in majority is $I \frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{2}{2} = 40$, in some, $I \frac{3}{3}C\frac{1}{1}P\frac{3}{4}M\frac{2}{2} = 38$. (*Ailurus*, red panda) or $I \frac{3}{3}C\frac{1}{1}P\frac{3}{3}M\frac{2}{2} = 36$ (*Potos*, kinkajou or monkey-tailed "bear"), or $I \frac{3}{3}C\frac{1}{1}P\frac{4}{3}M\frac{2}{3} = 40$ (*Ailuropoda*, bamboo bears or giant panda).*

¹Characteristics of the family, and later of the genus, are given briefly.

^{*}Now recognized as a true bear, not a procyonid-Sci. Ed.

Form of cheek teeth and character of their masticatory surfaces extremely variable. In one, they are powerful and broad with a flat multicusped, bluntly tuberculate masticatory surfaces, typical of omnivorous and phytophagous carnivores (extreme form is Ailuropoda, bamboo bear). Teeth in several are characteristic of meat-eating carnivores, of carnassial form with cutting crests. The fourth upper premolar and the first lower molar are transformed into carnassial teeth, resembling teeth of species of wolf family, Canidae (Bassariscus, cacomistles). In majority of species, cheek teeth of intermediate type—relatively broad and flat. Incisors rather weakly developed, the first premolar has tendency toward reduction—small or absent, sometimes disappearing with age. Canine relatively small.

The os penis is present and well-developed. Anal region devoid of glands and glandular areas.

As regards general appearance and size, species of the family are quite varied—with a small number of species in the group, differences are considerably larger than in other families of the order. One of the general aspects and dimensions is bear-like (Ailuropoda, bamboo bear), some are similar to cats (Ailurus, panda), others—fox and raccoon-dog (Procyon, raccoons) or weasel (Bassariscus, cacomistles) and some are quite individual (Nasua, coati; Potos, kinkajou or monkey "bears").

In some species, muzzle is short and obtuse; in others, it is of the fox or Arctic fox type, in still others, with very long pointed facial portion; in the majority of cases, ears quite large, rarely short and rounded; eyes usually quite large. In majority of species, tail long; in some, longer than trunk, covered with dense luxuriant hair; in one species, very short (as in bears), in another, strong, muscular and prehensile like a monkey's tail (*Potos*, kinkajou; a rare exception among carnivores). Pelage quite long and dense; in some, very dense, fluffy and long (raccoon, providing valuable fur).

Color entirely variable—from more or less monotone yellow or brownish to very mottled and bright, consisting of a combination of bright red with black (*Ailurus*, panda). In a series of species, dark transverse rings are well set off against the light general tone of the long, fluffy tail.

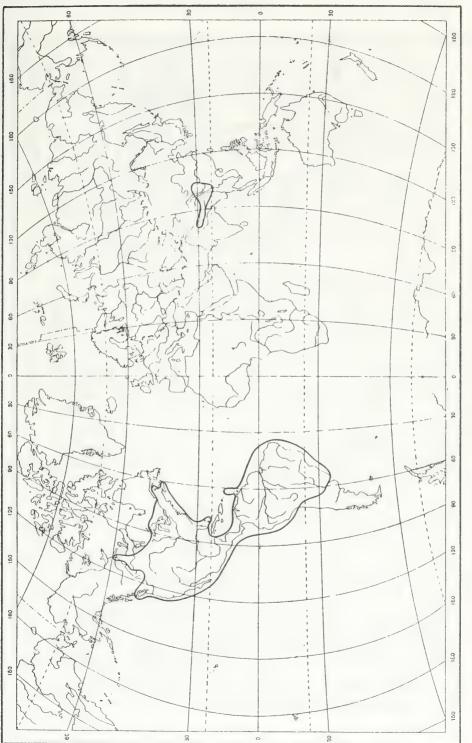
Differences in dimensions very great—smallest forms have body length of about 25-30 cm and about 1.25 kg in weight (Bassariscus,

cacomistles), and in the largest, head and trunk length is about 180 cm and the weight is about 150–160 kg (*Ailuropoda*, bamboo bear).

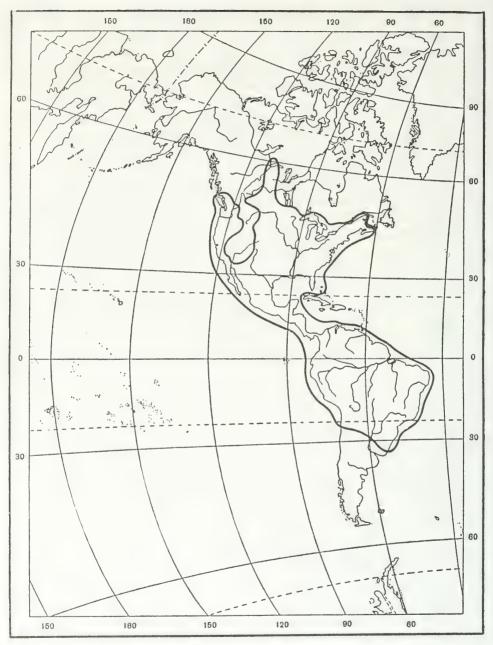
Species of the family are mainly in tropical, in part with warm temperate climates, and only one (raccoon) extends quite far into temperate zone, and in the north of its range even falls into winter sleep.

Some species ascend high into mountains and are even completely associated with montane regions (Asia—see below). All are, to a great or less extent, forest animals or associated with forest regions, the majority closely associated with forest, climb trees well and often, some live in tree hollows, etc. A series of species are mainly, arboreal animals (semi-retractile claws) or even specialized in climbing (monkey-bear, Potos). Some species are very fast and active, others are languid and slow in their movement. The majority are solitary nocturnal animals, forming only temporary family groups. One species is partly diurnal and sometimes forms large groups (Nasua, coati). The majority are omnivorous animals, chiefly "gatherers", feeding in addition to plant foods, on invertebrates and lower vertebrates, small rodents, birds, etc. Some are more predatory, a few are mainly phytophagous or specialize strictly on plants (bamboo bear, feeding on young shoots of bamboo).

The range of the family is divided into two parts—a vast American and relatively very small Asiatic. In America, the range occupies a considerable part of North America, except its northern part; Middle America; and a large part of South America, except its southern part. The northern borders of the range extend from the Gulf of Saint Lawrence, through southern Quebec, southern Ontario, the south of Manitoba and Saskatchewan, Alberta and through the south of British Columbia (for details, see below; description of raccoon). The southern border runs from the Pacific 910 coast of northern Chile (at approximately 20° S. lat.) to southeast to the mouth of the La Plata [river] on the Atlantic coast. The range includes Vancouver Island and several small islands lying directly along the shores of the southern part of North America, some of the Bahamas and Lesser Antilles islands (see below, species description) and Trinidad. In Asia, the range occupies the Himalayas in Nepal and Sikkim, and farther to the east upper Burma, Yunnan and north to the border of Gansu (an entirely montane region).



909 Fig. 344. Range of raccoon family, Procyonidae. In Asia, range of bamboo bear, Ailuropoda M.-E. and panda, Ailurus F. Cuv., usually associated with raccoons. V.G. Heptner.



910 Fig. 345. Range of the raccoon genus, *Procyon Storr**. V.G. Heptner.

*Misspelled "Starr" in Russian original—Sci. Ed.

The family Procyonidae in all of the diversity of forms admitted into it, according to the present point of view, represents a systematically diagnosed and well-defined group, which is sufficiently connected by common origin. Actually, this is, in substance, the broadly accepted opinion. The diversity of forms within the family must, apparently, be considered as an adaptive divergence, associated with feeding characteristics, and different degrees and forms of adaptations to climbing.

At the same time, diversity of structures within the family, led and sometimes still leads, to strong fragmentation. Separate authors divide it into 2, 3 and even 7 separate families. In the latter case, each well-defined genus is separated into a distinct family. There has also been no lack of division of the family into a series of subfamilies.

For example, several authors not only separate the genera *Potos* (kinkajou) and *Bassariscus* (cacomistle) from the family, putting them in the rank of separate families, but also entirely rejected the idea of close relationship with remaining Procyonidae. The systematic position of the genus *Ailuropoda* (bamboo bears) has been, and is, frequently treated in various ways. It was related to bears, separated into a special family (alone or together with the panda, *Ailurus*), and only relatively recently, it was again recognized as a member of the raccoon family.*

Having gone far, the subdivision of the raccoon group, as with anything to such detail, does not bring utility and only obscures the general picture of family structure and its relation to others. Evidently, it is more natural to consider a single family, Procyonidae, composed of two recent subfamilies (see below).

In the circle of families of the order, and the group Canoidea, the family Procyonidae shows the clearest relationship to the bear family, Ursidae (see characteristics of this family). Relationship to the wolf family, Canidae, is regarded as much less close, although some data also point to a certain relationship between these groups (see characteristics of wolf family, Canidae, and of genus of raccoon dogs, *Nyctereutes*). Also, there appear to be no clear relationships between the raccoon family and the marten family, Mustelidae. In the series of families of the order, the raccoon family is usually

^{*}Presently Ailuropoda is considered a bear-Sci. Ed.

placed as the immediate neighbor of bears and between bears. Ursidae, and martens, Mustelidae,*

The raccoon family is less ancient than the wolves, Canidae. and is associated, apparently, by its origin, with early forms of the latter. The main—American—branch of the family split off in the lower Miocene in the Americas, and throughout its entire history, it was restricted, as at present, to South and North America, generally within the boundaries of the present range. The Asiatic group is known from the upper Miocene, and throughout its entire history was much more widely distributed than in the present epoch, and in particular, the range included not only several parts of Asia. lying outside its present range, but also Europe. In the zoogeographical sense, and partly also the systematic, the Asiatic forms must be considered as relicts.

The family is divided into three subfamilies—one extinct American (Cynarctinae) and two contemporary—Procyoniae, the American raccoons and Ailurinae—the Asiatic raccoons or pandas. The total number of genera is 18, of which 8 are contemporary. The number of described species of contemporary American genera is quite great, however, most of them undoubtedly constitue only races and the total number of species is, probably, only 11 or 12.

The subfamily of American raccoons, Procyoninae, includes the genera: Bassariscus ("Jentinkia"**) (cacomistles; 2, possibly 3 species), Procyon (raccoons, 2 species), Nasua (coatis, 1 species), Nasuella (mountain coatis, 1 species), Potos (kinkajou, or monkey bears, 1 species), Bassaricyon (1, possibly 2, species).

The subfamily of Asiatic raccoons or pandas, Ailurinae, consists of the genera-Ailurus (panda, or cat bear, 1 species) and Ailuropoda (bamboo bear or giant panda, 1 species). Species of the family constitute in all 5% of the total number of species of the order. Equally with hyaena and bears, this family is one of the least specious families of carnivores.

912 In practical terms, a series of species are innocuous, some may be harmful to hunting economy, and individual species are considered valuable fur-bearing species or game animals (raccoons).

In the fauna of our country, indigenous representatives of the family are absent. One representative of the raccoon genus, Procyon has been acclimatized as a fur-bearing species (V.H.).

^{*}Appears to contradict statement in previous sentence—Sci. Ed.

^{**}Misspelled "Yentikia" in Russian original-Sci. Ed.

Subfamily of American Raccoons Subfamilia Procvoninae Gill, 1872

Genus of Raccoons

Genus Procyon Storr, 1780

1780. Procyon Storr. Prodromus meth. mamm., p. 37. Ursus lotor Linnaeus.

Size moderate.

In general appearance and body structure, the animal resembles the fox or, more closely, raccoon dog. Head broad, with sharp muzzle, ears large, protruding from the fur and tapering, tail fluffy, not prehensile, its length comprises about half, or slightly more, of body length. Digits long, deeply separated, grasping.

Skull moderately elongated, with broad braincase and well-defined crests. Hard palate extends far backwards—to 1/2 or 1/4 of total length of palate.

Dental formula $I\frac{3}{3}C\frac{1}{1}P\frac{4}{4}M\frac{2}{2}=40$. Molars and last upper premolar broad, more or less defined quadrate form, with flat masticatory surface and low, sharp protuberances. Carnassial teeth not developed.

Os penis present, to a greater or lesser degree curved.

Omnivorous predators, associated with forest regions, good tree-climbers. Northern forms in north of range fall into winter sleep.

A characteristically American genus, distributed in North America to the northern border of the range of the family (see characteristics of family above, and description of species below), and to the extreme, or almost extreme, southern limit of range of the family in South America—to southwestern Brazil, Paraguay, northwestern Argentina and southeastern Uruguay.

According to its systematic position within the limits of the family, the genus is quite closely related to several others and is not related to the number of those which show particularly sharp deviation. Both morphologically and biologically it is considered a generalized, apparently, a less specialized group of the family.

913

Within the limits of the genus, quite a lot of species have been described. Seven of them have been accepted at the present time by several authors. However, it is quite obvious, that there are in the genus 2 in all—the North and Central American *P. lotor* Linnaeus, washer-raccoon, and the South and Central American *P. cancrivorus* Cuvier, crab-eating raccoon. These sharply distinguished species are sometimes relegated to different subgenera (*Eupro-cyon*—for the southern species).

One of the species (northern) belongs among the most important fur-bearing animals of North America.

During the last decades, *P. lotor* was introduced into several European countries and into the USSR for acclimatization as a quality fur-bearing species (V.H.).

WASHER-RACCOON, OR AMERICAN RACCOON

Procyon (Procyon) lotor Linnaeus, 1758

1758. Ursus lotor. Linnaeus. Syst. Nat., ed. X, I, p. 48. Pennsylvania².

Diagnosis

Only species in the genus in the USSR.

Description

In general appearance—relatively short trunk, short legs, generally stocky build and dimensions—and in part in several characteristics of color, the raccoon, most of all resembles the raccoon dog, and, to a lesser extent, the red fox. Tail relatively short and constitutes about half the body length. Head short and broad with a short pointed muzzle and quite large eyes. Ears set wide apart, large and protruding strongly from fur, with moderately acute tips.

Winter fur long and fluffy, quite soft, with a thick underfur. Tail covered with long erect hairs and appears thick and fluffy. Upper surface of hands and feet clad in very short hairs—their pelage differs greatly from that on legs. Callosities on lower surface of paws bare.

²Further synonyms—very numerous—represent nothing of interest to us and are not provided.

General color tone of dorsal winter fur dull gray on the upper side, with greater or lesser admixture of brown, sometimes reddish or chestnut hairs (mainly on nape). Dark tips of hairs form slight wavy pattern against general fur color. On lower surface, general color tone slightly lighter; guard hairs here shorter and fewer and underfur more obvious. General tone of underfur grayish-tawny. Fore legs and thigh region have same color as lower body surface, hind legs higher*; their heels are blackish. Hands and feet lighter, almost white. On tail are 5 to 7 sharply defined black or brown rings, and its tip is black. Color of parts between rings (they are broader than rings) grayish or brownish. On lower surface of tail, dark rings not so sharply defined, their color lighter than on dorsally, and they are sometimes interrupted.

Top of head gray. On facial portion, black or nearly black 914 (brownish) "mask" sharply defined in form of large spot beginning on cheeks and extending, becoming wider, across eye to muzzle. Along upper surface of muzzle, it extends to lower part of nose forming narrow projection, which also extends backwards to forehead. Sometimes, stripe extending along muzzle slightly separated from eye spots by a slight brightening [see Fig. 346]. Facial mask is demarcated by well-defined white fields bordering it above and extending backwards under ears and to sides of neck. Lateral parts of muzzle, lips, chin and lower surface of lower jaw white. On throat, a transverse black or brown area, separated dark mask pattern; narrow white stripe which extends backward from muzzle. Ears clad with short grayish or brownish hairs and bear small black spots of varying size and definition at base of posterior surface.

In addition to the raccoons of the described normal color, black animals are met with (melanists).

There is one molt per year.

Facial region of skull short and quite wide. Braincase voluminous, obviously swollen from behind, long and wide in interzygomatic region with nearly parallel borders. Facial length of skull less than cranial. Nasal bones short and quite broad. Line of the upper skull profile convex—frontal region highest, from which profile line gently descends both backward and forward. Supraorbital processes very weakly defined, frontal surface between them somewhat concave longitudinally. Mastoid processes

^{*}Meaning unclear; hind legs longer?—Sci. Ed.



913 Fig. 346. Washer-raccoon, or American raccoon, *Procyon lotor L.* (Sketch by A.N. Komarov).

large; paroccipitals moderately developed. Hard palate extends behind end of toothrow to approximately 1/3 of total palatine length. Auditory bullae rounded in form, inflated. Sagittal crest weakly defined; occipital—well [defined]. Canines relatively short, upper almost straight, lower clearly curved. Fourth premolar and first molar of upper jaw almost equal to each other (molar a little larger),

second molar approximately twice less than first. First and second lower molars almost equal in dimensions.

Body length of males is 435-545 mm, of females, 410-570 mm; tail length of males is 200-405 mm, of females, 192-340 mm; length of hind foot (with the claw) of males is 96-138 mm, of females, 83-129 mm.

Condylobasal length of male skull is 94.3–125.8 mm, of females, 89.4–115.9 mm; zygomatic width of males is 60.2–89.1 mm, of females, 58.3–81.2 mm.

Weight fluctuates very greatly, particularly in connection with fat accumulation before winter hibernation—from 5.4 to 15.75 kg and may even reach 22.2 kg³ (V.H.).

Systematic Position

In comparison to the second species of the genus—*P. cancrivorus*, the described form is sharply characterized. In some respects, it is, apparently, more specialized (V.H.).

Geographic Distribution

Central and North America. Acclimatized in the USSR, Central Europe and on several islands of the West Indies.

916 Geographic Range outside the Soviet Union

Natural range occupies North America and Central America, southwards to the Panama Canal zone. The northern border of the range is quite complicated—starting at the lower reaches of the Saint Lawrence River (near Quebec [city]), it extends along the south of Quebec and Ontario (Canada) provinces to Lake Nipigon (a little north of Lake Superior), starts along the shore of Superior, going along it to its western extremity. Thence, it directs itself to the southwestern extremity of Lake Winnipeg, and farther, rises in a curved line northwards to the western part of Lake Athabaska. Thence, the border sharply descends to the south-southwest—to

³There is very little information on dimensions and weight of raccoons acclimatized in our [country], and they do not give a correct idea about variation in these characters. Figures given above are from American sources and characterize variability of the species in its native land in general. Size and maximum weight after Hall and Kelson (1959), remaining data on weight after Burt and Grosenheider (1952).

the southwestern corner of Alberta Province. Farther, the border takes a completely curious form. It describes a large extension, a loop as is were, to the south, bypassing a significant (eastern) part

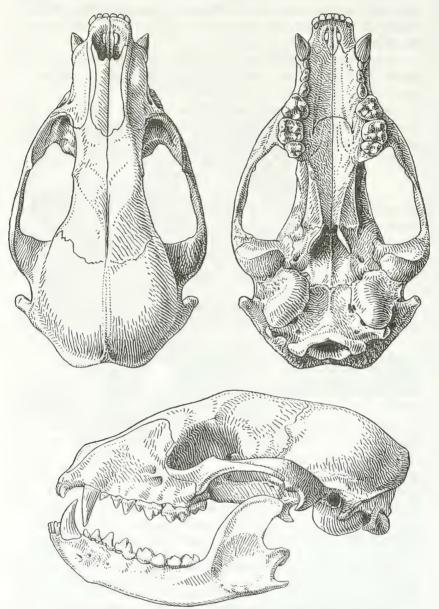
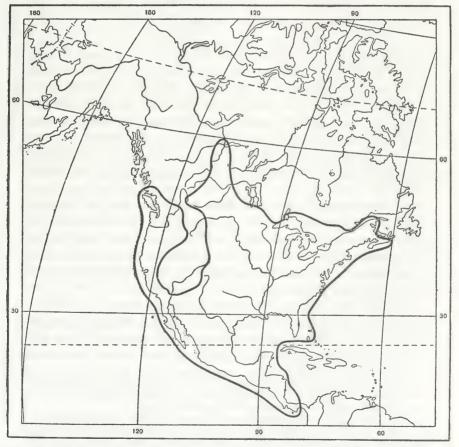


Fig. 347. Skull of washer-raccoon, or American raccoon, Procyon lotor L.

of the Rocky Mountains and Great Basin and descends to 40° and even 35° N. lat*. From this region, being drawn towards the Pacific Ocean the border passes northward, sometimes near it (southern), sometimes strongly distanced (northern), to the southeastern corner of British Columbia and, rising somewhat to the northwest, reaches the coast of the Pacific ocean at the level of the northern extremity of Vancouver Island.

In the Pacific Ocean, the range includes Vancouver Island and the small islands of Las-Tres-Marias along the Mexican coast. In the Atlantic Ocean, it is encountered on small islands lying directly off the coasts of South Carolina, Georgia and Florida.



916 Fig. 348. Natural range of *Procyon lotor L.* Somewhat simplified. Habitats in the Archipelago of the Windward Islands are not shown (after Hall and Kelson, 1959).

^{*}The species range now includes most of this region—Sci. Ed.

Generally speaking, raccoons are absent on islands of the West Indies; however, they are found on some of the Bahamas (in particular, New Providence near Nassau⁴), on Cosumel Island near Yucatan, and on the Lesser Antilles Islands, in particular, on Guadeloupe and Barbados (possibly also others) from the Windward Islands.

The raccoon was acclimatized and lives in many parts of the F[ederal] R[epublic] of G[erman] and the G[erman] D[emocratic] R[epublic]. It was not introduced in other countries. Transgressions to Holland and northwestern France are known (Niethammer, 1963).

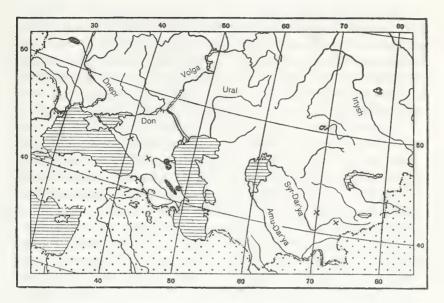
Geographic Range in the Soviet Union

The experiment in acclimatization of the raccoon in our country began in 1936, and was repeated more than once in various parts of the country. The total number of attempts (up to 1962) was 26 releases, for a total 1222 individuals. Of these, 64 were from the farms and zoos (38 imported from western Europe), the remaining were derived from a population which had been put together in the Trans-Caucasus (Zakatalo-Nukhinsk valley in Azerbaijan; Rukovskii, 1963). The animals were introduced in various places, often far from each other, and they never formed a significant, continuous range. Far from all of the transplantations (with respect to the purely biological side of the matter) had the same results. In several places, the animals died, in others, the results have not yet been sufficiently determined or are unreliable, in several, the animals apparently survived well, obviously settled down and formed quite numerous populations⁵.

In the Far East, raccoons (black) were introduced on Petrov Island near Vladivostok and a series of places in Primor'e territory (southern half), but all introductions were unsuccessful—the animals died (on the map, these places are not shown; Abramov,

⁴The suggestion that raccoons appeared (were introduced?) on the Bahama Islands in 1932 (Niethammer, 1963) was based on a misunderstanding—*P. maynardi* was described as early as 1898 from New Providence Island.

⁵Concerning information given below on places and results of transplantation of raccoon in our country are based on the most recent, in part unpublished, data and describe the situation in 1962 and the beginning of 1963. They differ significantly from Kolosov's (1958) and Rukovskii's (1960) communications, in which the success of acclimatization was strongly overstated and already did not conform with the actual situation.



917 Fig. 349. Localities of introduction and occurrence of the washer-raccoon or American raccoon, *Procyon lotor* L., in the USSR. Places where acclimatization was unsuccessful or results unclear, are designated by crosses; places where the raccoon apparently survived—by dots, and the districts in Byelorussia and in Azerbaijan, where more or less stable populations were constituted, are designated by blotches (V.G. Heptner).

1963). In Middle Asia, raccoons were introduced into former Dzhelalabad district of Kirghizia, in the nut and apple forests of the southern slopes of the Tien Shan Mountain Range—facing towards the Fergana valley—in Arslanbob (north of Dzhelalabad).

918 They were noted here in the Ach'region (between Arslanbob and Dzhelalabad) and in the Bazar-Kurgan region (west-northwest of Dzhelalabad; introduced in 1936 and 1952; Novikov, 1956). In January 1963 here "raccoons are practically absent". Raccoons were introduced into the mountain forests of the valley of the Pskem River (near kishlak* Sidzhak northeast of Tashkent, between the Ugamsk and Pskem ranges—the extreme western spurs of Tien Shan; Salikhbaev et al., 1963).

⁶P. Sagaraev, Board of Forestry and Nature Protection belonging to the Council of Ministers of the Kirghiz Soviet Socialist Republic. Apparently, these introductions (in Chavachin and Karaamin forest farms; their location is imprecise), and Yanushevich (1963) also spoke of them, believing that these introductions were not successful, recommending cessation of raccoon introduction in Kirghizia.

^{*} Local word for village-Sci. Ed.

According to one datum of Salikhbaev et al. (1963), the raccoon survived here, and has somewhat broadened the area of its occurrence; according to other data—"the results...were unclear", and evaluation of its situation and its future fate is too optimistic in the literature. On the whole, attempts to acclimatize the raccoon in Middle Asia have been unsuccessful or their results as of 1963 are not clear and, apparently, they must be stopped.

In the eastern Trans-Caucasus (Azerbaijan), introduction of the raccoon into the forest zone associated with the southern slope of the Main Caucasus range, beginning in 1937, was successful and led to the creation of a quite considerable and stable population (annual catch of 1000–1500 individuals), occupying one quite significant section, and isolated centers separated from it. The main range extends as a strip from the region of Belokana City (a little east of Lagodekha) along the so-called Zakatalo-Nukhinsk forest (Zakatalo-Nukhinsk valley) to Nukha city, and farther, to the Ismailla region, *i.e.* for an extent of more than 200 km. This region is the largest focus of occurrence of the species in the USSR, from whence is taken material for future settlements.

A separate section of occurrence is found in the so-called Kuba-Khachmas forest massif—from Kuba toward the northeast and north to Khachmas and Khudat on the railway line near the sea shore. At the beginning of the 60's, this section was apparently not yet connected with Zakatalo-Nukhinsk. A small section of occurrence lies in the Talysh and Lenkoran forests. On the whole, in 1963 in Azerbaijan, the raccoon inhabited Belokansk, Zakatal'sk, Kakhsk, Nukhinsk, Vartashensk, Kurtkashensk, Ismaillinsk, Khachmassk and Lenkoransk regions (Ya.K. Aga-Zade, Nature Protection Board of the Council of Ministers of the Azerbaijan SSR).

In the North Caucasus, the raccoon was introduced, and apparently, survived, in the riparian forest of the Terek and along the Sulak [river]? in the lowlands of Dagestan (south of the eastern Cis-Caucasian lowland). Raccoons were introduced along the "left tributary of the Kuban'" (Aliev, 1963), but clear data about them are absent. The attempt to settle raccoons in Kabardin-Balkariya (black raccoons) was unsuccessful.

As shown by an almost ten-year experiment, attempts to acclimatize the raccoon in Byelorussia were, apparently, quite success-

⁷M. Isamukhamedov, Board of Forestry and Nature Protection of the Council of Ministers of the Uzbek. SSR.

ful, where, as a result of three introductions (52, 37 and 38 individuals in 1954 and 1958), a significant population was formed (on 1 January 1963, about 700 individuals). It occupies a section along the Pripyat' River from Petrikov up almost to Pinsk (about 120 km), approximately 30 km in breadth along each bank (Petrikovsk and Zhitkovichsk regions of Gomel'sk district, and Stolinsk region of Brest district⁸). The situation of the population has been evaluated as satisfactory.

Information in the foreign literature (Niethammer, 1963) concerning the occurrence of raccoons in Latvia (in spring 1961, 7900 individuals!), is completely untrue. In Latvia, the raccoon-dog is widely distributed, but the raccoon was not introduced at all.

The perspective on raccoon acclimatization in our country, if the Caucasus—mainly the Trans-Caucasus—is not considered, Trans-Caucasus, is very limited from the purely biological side, although steps already undertaken have not yet been sufficiently studied. The economic side has also not yet been analyzed (for details, see section "Biology") (V.H.).

Geographic Variation

American authors, even the most recent, believe that geographic variation of the raccoon is very extensive. Some accept 30 races of the species *P. lotor*, and another 4 species (insular) besides *P. cancrivorus*, accepted here (Miller and Kellog, 1955); others recognize 24 races of *P. lotor* and another 5 species (one with two races), besides *P. cancrivorus* (Hall and Kelson, 1959). These considerations are, apparently, exaggerated.

It is not known which forms were introduced into our country. As said, part were derived from the zoological parks and fur farms (V.H.).

Biology

Population. Experiments in acclimatization of the American raccoon first began in 1936, when the Uzbek Zoo introduced 22 raccoons in former Achin region of the Kirghiz SSR. In 1949, their number here did not exceed 80–100 individuals, with a density 5–8 animals per 1000 hectares.

919

⁸A. Abaturin, State Committee for the Nature Protection of the Council of Ministers of Byelorussian SSR.

An experiment in introduction of two pairs of black raccoons on Petrov Island in Primor'e territory in 1937 proved unsuccessful. In 1941, 21 raccoons were introduced in Ismaillinsk region, Azerbaijan SSR (Rukovskii, 1951). In 1950, it was established that they already inhabited a series of regions in an area of 1300-1400 km². The total number of raccoons reached 2000 individuals, with density averaging 15.3 animals per 1000 hectares. In 1950, 44 raccoons were introduced into the Khuzakhsk and Khasav"vurtsk regions of Dagestan. In 1951, 28 raccoons were introduced 70-90 km to the south of Krasnodar city. In 1952, 33 raccoons were introduced into the former Oktyabp'sk region of Kirghizia, and 79 raccoons into the Zakatal'sk region of Azerbaijan SSR. In 1953, in former Khizinsk region of Azerbaijan, 17 raccoons were introduced, while 43 raccoons were settled in former Bastandaksk region of Kazakhstan, and 16 black raccoons-in Kabardinsk A[utonomous] S[oviet] S[ocialist] R[epublic] south of Nal'chik in the region of the Nal'chik and Belaya rivers. In 1954, 50 raccoons were introduced in Petrikovsk region of Gomel'sk district of B[velorussia] SSR, 55 raccoons in former Budennovsk region of Primor'e territory, and 104 raccoons—on Zelenchuk river in Stavropol' territory. In all, from 1936-1954, 534 raccoons were introduced for acclimatization. From 1941, all introduced animals, except 16 black raccoons, were caught in the Zakatalo-Nukhin valley of Azerbaijan (N.N Rukovskii).

In 1954, 486 raccoons (Abramov, 1961) caught in the Trans-Caucasus were introduced in Partizansk, Anuchinsk and Yakovlevsk regions of Primor'e territory. The introductions were accomplished in coniferous—broad-leaved forests in the valleys of montane taiga rivers. In these forests there was extensive tree-felling and forest fires, trees with hollows were few, and food resources were insufficient. The raccoons went off to the lowlands, but there, tree hollows were also few, and the raccoons settled in burrows, clefts of rocks and haystacks. They were not able to accumulate fat before winter and they spent the winter badly (its duration is 120–150 days) with severe frosts. Mortality was recorded among them from hunger and cold. In following years, the population everywhere was less than in the year of introduction. Reproduction occurred locally, but mortality was greater. In the 60's, the raccoon became extinct in Primor'e.

In Krasnodarsk territory (Kotov and Ryabov, 1963), raccoons settled in a narrow belt with an area of about 7000 km², extending from Novorossiisk to Lazarevskaya. Here, they were sporadically 920 encountered everywhere in low density. In better places—in Gorvache-Klyuchinsk region—3.5 animals per 1000 hectares; in the Gelendzhiksk region—0.6; in Lazarevsk region—0.1. In more favorable lands of the Ismaillinsk region, density reached more than 20.0 animals per 1000 hectares (Rukovskii, 1951). In their native land, in boggy lands of Wisconsin state (USA), density of raccoon settlement fluctuated from 25.7 to 34.6 per 1000 hectares (Dorney, 1954). Under more favorable conditions of the southern states, raccoon populations may attain a very high density. Up to 1949, their highest density was considered to be established in Illinois; in an area of 384 hectares—111.0 animals per 1000 hectares, but in the state of Missouri, 102 raccoons were caught in an area of 25 hectares; i.e. here their density was 408.0 (Twichell and Dill, 1949). In the state of Ohio (Butterfield, 1944), in open hunting lands, were established densities of: 36.1; 142.0; 166.6; for reserves—340.0 (66 raccoons on 193.5 hectares).

Habitat. In Kirghizia, raccoons inhabit montane forests dominated by walnut trees. In the Trans-Caucasus, they prefer valleys with broad-leaved forests consisting of oak, white-leafed poplar, smooth-leaved elm, alder, walnut and chestnut. In these forests, there are many lianas, wild almond-leafed willows, hops and hollow trees. Raccoons no less willingly settle in montane beech forests almost devoid of undergrowth (N.N. Rukovskii).

In the USA (Nelson, 1930), raccoon—one of the few wild animals, whose populations increases with cultivated appropriation of territory. With free water and forest vegetation, raccoons here settle also in the swamp lands (Dorney, 1954); the presence of trees of large diameter with hollows are preferable but not necessary.

Food. The American raccoon belongs to the group of omnivorous predators. In composition its food includes a variety of both animals as well as plants. Their combination, and the ratio of each, depend upon the biotope, time of year, and the yield of each food (see Table 71).

In the northern USA, in swamp lands of the state of Wisconsin (Dorney, 1954), the raccoon's main food consists of crustaceans, fish, young muskrats, insects, grapes, fruits and berries (see Table 72).

Table 71. Seasonal characteristics of raccoon nutrition in Texas (% of occurrence. Becker, 1945)

Type of food	Spring	Summer	Autumn	Winter
Birds	4		_	_
Snakes		2		_
Fish	4	4		4
Freshwater crustaceans		_		
Mollusks	4	3		
Wasps	_	_	23	
Beetles	18	22	21	_
Crickets	3	16	10	
Larvae and pupae of butterflies	s —		_	7
Spiders	_	_	_	7
Water scavengers, and diving beetles	_	9	_	_
Water bugs	_	16	_	
Acorns	55	47	29	57
Wild grape		38	24	- California
Mulberry	14	2	6	_
Persimmon	_	10	36	10
Hawthorn		3	6	13

921 Table 72. Seasonal characteristics of raccoon nutrition in Wisconsin (% occurrence)

Food type	III–IV	V–VI	VI–VII	IX-X	X-I
Adult muskrats	20	6	2	2	12
Young muskrats		40	35	9	
Cricetid rodents	10	11	2.	1	
Adult ducks		1		1	12
Duck eggs		7	3	1	
Eggs of other birds	_	4	1	_	
Fresh water	49	52	64	64	6
crustaceans					
Fish	20	17	3	22	25
Frogs		1		_	_
Insects	7	27	16	5	
Maize	39	8	1	11	50
Acorns	2			9	
Grapes	_	_	8	60	_
Wild pear			10	14	
Raspberry			19		

The frequency of young muskrats in the raccoon diet in various swamplands fluctuates from 8–9 to 19% (Dorney, 1954). In the state of Washington (Tyson, 1950), the occurrence of mollusks in the diet of adult raccoons in summer was 85%, of crustaceans—85%, of fish—65% and of neris worms*—50%. In the stomachs of

^{*}Meaning not clear; probably refers to marine polychaetes—Sci. Ed.

young raccoons, mollusks constituted 67%, crustaceans—100%, fish—45%, worms—11%, milk—78% of the contents (20 stomachs of adults and 9 of young).

In the Trans-Caucasus (612 excrement samples; Rukovskii, 1951, 1957); the raccoon feeds mainly on the following kinds of food (% of occurrence):

Mammals	5.5	Fish	2.3
Birds	11.7	Crabs	2.6
Amphibia	52.6	Insects	82.4
Reptilia	13.2	Mollusks	12.9
•		Plants	63.9

Therefore, under new conditions, the raccoon shows itself to be a typical polyphagous animal, like the badger as regards food habits. Of mammals, it feeds on mice and voles; of birds—mainly on small passerines and injured ducks. Of reptiles, raccoons eat turtles, lizards, rarely snakes; of amphibians—Trans-Caucasian frog. Among insects were encountered beetles, orthopterans, lepidopterans, dragon flies and caddis flies, among them a significant number fall among pests of agricultural plants—mole cricket, locusts, crickets, long-horned beetles, bark beetles, click beetles, leaf beetles, weevils and others. Raccoons feed also on plant foods: in the Trans-Caucasus, most frequently wild grapes, fruits of lianas (sasparilla), nuts and acorns. To a lesser extent, they eat pears, apples, cherry plum and blackthorn. In spring and winter, raccoons utilize more animal food, in summer and autumn—plants.

Home range. Dimensions of the home range of the adult raccoon are associated with the abundance of food within its borders and the distance of feeding areas from shelters. In Azerbaijan (Rukovskii, 1951), the area of such a home range fluctuates from 4 to 9 km², with a radius of 1.0–1.5 km from shelter. A lactating female does not travel more than 600 m from her litter. Consequently, the area of her home range does not exceed 144 hectares.

In the state of Ohio (USA), during two years, no cases were recorded where a raccoon traveled more than 1.5 km from the place it was marked (Butterfield, 1944; according to recapture of 91 marked raccoons). On average, the animals were caught no farther than 400 meters.

Burrows and shelters. In Azerbaijan, the raccoon settles in hollows of white-leaved poplar trees, rarely oak (Rukovskii, 1951,

922

1955). This is explained by the fact that hollows of size suitable for raccoon, are here more frequent in poplars. Average height of hollow trees inhabited by raccoons is about 21.0 m, their circumference (at breast height) reaches 4.5 m. The living cavity is situated at a height of 10–12 m from the ground. The average diameter of the entrance hole is 19 cm (not less than 12 cm). Amplitude of daily temperature fluctuation inside such a cavity does not exceed 3.5°C, and in hot summer hours, the temperature is 10–12°C lower than that of the outside air. Besides the main living hollow, within the home range of the raccoon, there are also temporary shelters—hollows, where the raccoon spends the day resting.

In North America, raccoon also settles in caves and among rocks and clefts. In the absence of tree holes, it settles in earthen burrows, muskrat huts, boxes for nesting ducks and other shelters (Dorney, 1954). During the capture of 297 raccoons in the state of Ohio, only 8% of them were hidden in tree holes, 47.5%—among rocks and in burrows, the remainder—under roots of trees, on newly fallen trees, etc. Of 316 raccoons, 46.4% occupied ground burrows, 18.2%—tree hollows, 14.4%—shelters in the base of trees, and 10.0%—among rocks. Raccoons occupied 22% of the artificial bird nests of the box type (Butterfield, 1944).

Raccoons often occupy burrows of marmots, sometimes in open places. Litters were also found in haystacks and heaps of brushwood. It is supposed that the raccoon was initially a species closely associated with tree hollows. As a result of cutting down large-trunked trees containing hollows, and the transformation of forest areas into agricultural ones, the raccoon became an animal capable of living under various conditions of cultivated landscapes.

Daily activity and behavior. The raccoon is a crepuscular-nocturnal animal. It emerges from its hole at sunset and sometimes returns to it even at day break. It climbs trees well, but it gathers its food mainly on land—along river banks, in swamps and other similar places. In searching for food, it sometimes rambles through shallow water and along sand bars.

A characteristic feature of the raccoon is that it rinses its gathered food in water before eating it. Hence, the raccoon's name "poloskun", (= to wash off).

Hibernation and winter sleep. In districts with snowy, cold winters, the raccoon, as well as the brown bear and badger, have a characteristic winter sleep. In the Trans-Caucasus (Rukovskii,

1951), in association with warm winters and brief frost, raccoon activity stops only during snowfall. It emerges when the soil is partly free of snow. In Kirghizia and Canada, where snow lasts for a longer time, raccoons leave their shelters earlier, before the snow thaws in spring. In Canada, their sleep lasts for about four months of the year. Here they are able to survive hollows while the temperature of the outside air is down to -43°C.

Seasonal migrations and transgressions. After the introduction of 250 raccoons from Ohio into Arkansas, their appearance was noted 37, 75 and 255 km from the place of introduction (Butterfield, 1944).

Reproduction. In Canada, i.e. in the northern parts of the range in America, estrus occurs is March. In yearling females, estrus takes place in May-June. In the state of New York, raccoons mate at the end of January-beginning of February (Mackeever, 1958). In the state of Michigan, the majority of females mate in February-beginning of March, and few of them—at the end of March; individual cases of mating were observed in Virginia at the beginning of June.

In the states of Florida and Georgia, the season of reproduction lasts from 10 February until 3 August: in February, 14% of the females are mated, in March—41%, in May—12%, in June—12%, in July—12% and in August 6% (Llewellyn, 1953*). After a pregnancy lasting for 63 days, raccoons bring their young into the light in the period from April to the beginning of October. Practically half of all [parturition] occurs in May. The number of embryos averages 3.2, fluctuating from 2 to 5. In the state of Michigan, the average number equals 4, with fluctuation from 3 to 7.

In the Trans-Caucasus, young appear in April-beginning of May. The quantity of newborns fluctuates from 3 to 8, more frequently 4 (Rukovskii, 1951).

Growth, development and molt. On the 21st day of pregnancy, length of the embryo reaches 24 mm, on the 35th day—45 mm, and on the 46th day—65 mm (Llewellyn, 1953)**. Young are born blind, and eyes open on the 20th day. At 1.5 months of age, they cut all teeth. At the age of 2.0–2.5 months, they already accompany their mother while searching for food, and at 4–5 months old, they switch over independent foraging. In September–October,

^{*}Not in Lit. Cit.-Sci. Ed.

^{**}Not in Lit. Cit.-Sci. Ed.

young raccoons do not yield, in terms of dimensions, to adults, but are markedly lagging behind them in weight.

Raccoons attain sexual maturity at the age of about one year. Sex ratios in populations are different: in the states of Ohio and Illinois, the ratio favored females—46:54 and 40:60 (among hunted animals, even 14:86), in the state of Missouri—(62:38 and 61:39, *i.e.* the ratio favored males).

Out of 102 raccoons caught in an area of 25 hectares, 32 were alone, and in 12 cases caught in pairs; in 6 cases the raccoons were obtained in trios. Only one time were groups of 4, 5 and 6 raccoons were caught. The animals were caught in winter during winter sleep (Twichell and Dill, 1949).

Enemies, diseases, parasites, mortality, competitors and population dynamics. Wolf, lynx and eagle-owl are regarded as enemies of the raccoon. In places inhabited by raccoons in the USSR, these predators are rare and do not cause great losses to it. There are no data on diseases and mortality of raccoons. In Trans-Caucasus, competitors of the raccoon in obtaining food are shown to be brown bear, badger, otter, pine and stone martens, jackal, cats, wild pig, red deer and fat dormouse (Rukovskii, 1951, 1953).

There are no data on population dynamics. In Kirghizia, the raccoon population increased 5-fold within 13 years, and in Azerbaijan—100-fold within 9 years.

Field characteristics. The crepuscular-nocturnal activity of the raccoon makes it very difficult to carry on direct observations. Their presence may be known by the characteristics of inhabited hollow (claws marks on bark, polishing of entrance into tree-hole, etc.) and by the tracks of their paws on damp soil along the banks of water bodies. In the track of the anterior paws, prints of five long clawed digits are clearly seen. Tracks of the hind paws resemble, in strongly reduced aspect, tracks of the hind paws of brown bear. They are more extended in length than in the badger (P.Yu.).

Practical Significance

The American raccoon is a valuable fur-bearing animal. Its hide is mainly used in the manufacturing of men's winter fur coats. In view of the fact that the districts of its probable distribution should, apparently, be restricted to the zones of mixed and broad-leaved

forests, the practical significance of raccoon as a fur-bearing animal cannot be great. Its practical importance may be more considerable in the southern regions of the USSR, where objects for fur manufacture are few. With occupation by raccoons of marshy lands, they may cause losses to young muskrats. Raccoons do not pose any danger to adult muskrats and aquatic birds since they only feed on injured individuals. Raccoons are useful as they destroy insects harmful to forests and agriculture. (P.Yu.).

Family of Mustelids

Family Mustelidae Swainson, 1835

AMERICAN MINK¹

Mustela (Mustela) vison Schreber, 1777

- $1777.^{2}$ Mustela vison Schreber*. Die Säugethiere pl. 27. Eastern Canada.
- 1949. Mustela vison tatarica Popov V.A. Tr. Kazansk. Filiala AN SSSR. Seriya biol. i s-kh. nauk, 2, p. 135. Tatari.
- 1958. Lutreola vison altaica. Ternovski. Biologiya i akklimatizatsiya amerikanskoi norki (Lutreola vison Brisson) na Altae (Biology and acclimatization of the American mink ... in Altai), p. 15. Middle course of Sary-Koksha River, Altai. (V.H.).

Diagnosis

Color and skull are same as in Russian mink, Mustela (Mustela) lutreola, but upper lip has same color as top of head (not white) and postorbital constriction of skull is sharper—its width is less than width of interorbital area. Dimensions somewhat larger (V.H.).

¹In our literature, this species is sometimes called the "eastern mink". There is no basis for the introduction of this new, completely artificial name. This name also is confusing-the range of the American mink, with respect to the European, lies nearer to the west, in the western hemisphere.

²Some of our monographers (Novikov, 1939, 1956; V. Popov, 1949; Ternovskii, 1958) refer to Brisson as the author of this name with reference to 1756, and they even try to designate the priority of this assignment to Schreber. This is a clear misunderstanding. Zoological nomenclature begins in 1758 (publication of the 10th Edition of "Systema Naturae" by Linnaeus) and all names given earlier are generally not accepted.

*Mispelled Schreder in Russian original-Sci. Ed.

924

Description³

In general appearance and construction, the American mink is completely like the Russian; however, the tail is on average somewhat longer, and reaches or almost reaches half the body length (from 38 to 46 and even 51%).

Winter fur is as in the Russian mink, but denser, close-fitting, longer, more luxuriant and softer. As fur, its value is higher than fur of the European mink. Length of contour hairs (Altai) on back is 27.7 mm, on belly is 22.2 mm, guard hairs are 22.7 and 16.6 mm, underfur is 14.8 and 10.6, respectively. Number of hairs on 1 cm² on sacrum is 19,530; on shoulder, 21,783 and on the belly 17,320 (Tserevitinov, 1958).

According to other data, in Altai mink (4 specimens) (Ternovskii, 1958), number of hairs on 1 cm² in middle of back ranges between 22,664 and 37,100, consisting on average about 22,458. For one guard hair, there are from 31 to 34 underfur hairs. Length of guard hairs on back is 20.9 mm, of underfur hairs, 12.3 mm.

There is one pair of inguinal teats, and three pairs of abdominal, in all eight; as an exception, six.

General tone of winter fur tawny of various intensity, from very dark blackish-tawny to light-tawny. Color is equally distributed over all of body, lower side only slightly lighter than upper.

Guard hairs, bright, dark-tawny, on spine often approaching black, straight and elastic, but not coarse. Underfur hairs on dorsal part very wavy, grayish-tawny with a bluish tint. Base of underfur 925 is light bluish-gray. Tail darker than trunk, and closer to tip, intensity of dark tone strengthens, and sometimes end of tail has pure black color. Sometimes, along the back, a broad wash of somewhat darker stripe is displayed. Chin and lower lip white—white color does not spread onto upper lip as a rule.

Color exhibits quite significant individual variability, which may be somewhat different in populations comprising various parts of our country. This applies to both qualitative and quantitative aspects (for cause, see section "Geographic Variation"). Percentage ratio of different saturated color types varies in different

³All data given below, especially where no individuals are preserved, belong to populations from natural conditions within the USSR. Best known are populations in the Tatar Republic (V. Popov, 1949); Altai (Ternovskii, 1958); in others data are very scarce and fragmentary.

populations, but dark and very dark animals predominate. Thus, in Tatariya, tawny-black animals constitute 48%, dark-tawny 36%, tawny 10% and the light-tawny 6%. Frequently on skins (in Tatariya, about 24%) white guard hairs ("hoary") are encountered and sometimes the tail tip is white (in Tatariya, about 4%).

In some individuals, underfur is white in color and may occupy from 40 to 80% of skin area, or they may even be distributed on the entire body surface. In addition to white lower lip and chin, very often there are irregular white marks noted on the lower surface of the body—on throat, neck, chest, belly and groin. They lie along the mid-line of the animal venter in the form of patches and sometimes stripes. The number of patches and the area they occupy vary. In the Altai, 29.2% of them were on the lower lip and throat, in 30.4% they extended from lower lip to fore limbs, in 35.1% they extended from lower lip to anus, in 4% they were distributed on the groin, in 0.1% between fore paws, in 1.2% on lower lip, throat and groin, and in 0.1% on chest and groin. It is noteworthy that the white marks may sometimes (3.3%) not occur



925 Fig. 350. American mink, Mustela (Mustela) vison Schreb. Sketch by A.N. Komarov.

at all (data from 727 skins). As a rule, the upper lip in the American mink is never white. However, in the Altai, in 36.4% (213 skins of 585) white patches occurred on the upper lip. Their dimension varies from weakly defined to those occupying more than half the lip. In Tatariya, this is absent. In the Altai, the white marks are, apparently, more strongly developed than in other regions of our species range. A broad white patch (as in marten) on the neck and chest, is rarely encountered in the Russian mink M. (M.) lutreola; in our American mink, it has not been mentioned.

Considerable development of white patches is characteristic of cage minks. It is very interesting that in Tatariya, with naturalization of the animals, within 10–11 years, the number of skins with white patches on chest, belly and groin, decreased sharply. At the end of this period (1938–1948), only animals with small white patches and only on lower lip, chin and throat were found (V. Popov, 1949). Apparently, there was a gradual elimination of this feature.

The animals in which the ends of the guard hairs are twisted, similar to singed hairs, are rarely met with. This "singing" is a mutational deviation known from caged animals in the Altai (7.8%). On the whole, color variation of American minks inhabiting the USSR is much greater than in Russian [mink].

Sexual differences in color and in development of patches and hoariness are absent. The latter is more often developed, either in males (Tatariya) or in females (Altai, 94.6%). White underfur apparently occurs more often in females. Hair length in females is approximately 2 mm less than in males (middle of back, V.A. Popov, 1949).

Summer fur of our [American] mink has not been described in detail. Its color differs little from winter, but is shorter, sparser and dull. Length of summer guard hairs on dorsum is 17.3 mm, and that of underfur—9.8 mm; on 1 cm² of dorsum there are about 17,450 hairs on average, for 16–22 underfur hairs for each one guard hair (Altai).

The skull is similar to that of the European mink, but it is more massive. It is narrower and less elongated, cranium is wider, shorter and more flattened. Postorbital constriction is more sharply defined—in narrowest part, its width is greater than width of skull between orbits. Zygomatic arches, especially in middle portion, are thinner and weaker than in Russian mink, but diverge somewhat

more widely. Mastoid processes well-developed and fuse with lower part of occipital crest. Auditory bullae are flat and broad; in posterior part they are set apart from each other not so far as in European species. Ratio of their length to their breadth approximately 1.0:1.5. Protuberances, crests, etc. of skull are generally more sharply-defined than in Russian mink; occipital crest developed significantly more strongly; sagittal crest—well[-developed].

Upper molar larger and more massive than in Russian mink, its area, in frontal projection, no smaller or only slightly smaller than area of upper carnassial tooth; longitudinal diameter of its well developed inner lobe more than logitudinal diameter of outer lobe. Posterior end of second upper premolar more or less strongly transgresses into notch found at anterior end of carnassial tooth. Inner surface of main cusp of lower carnassial tooth with well-developed sharp rib. On the whole, in its general appearance, specialization of skull as that of a predator skull more strongly developed than in Russian mink, and as regards degree of specialization itself, somewhat reminiscent of polecat skull.

Skulls of females, besides general dimensions, distinguished by somewhat less development of crests, protuberances, etc. and are somewhat lighter. Skulls of young are characterized by the more rounded and expanded braincase and weakly developed facial portion.

Geographic variation of the skull within the borders of our country not expressed (see beyond).

The os penis of the American mink, having a structure typical of the genus, differs considerably from that characteristic of the European mink, not only in size, but also in form. If one looks at the bone from below, its terminal part is not deflected to the right and the bone is curved in one plane. Its base is laterally compressed and is significantly wider along the vertical. Basal third is also flattened. Along middle of sides, there is a short groove, and on lower surface of the anterior part, there is a deep groove (Novikov, 1956; V. Popov, 1949). There are 14 thoracic vertebrae, 6 lumbar, 3 sacral and 18–21 caudal (40 individuals). Weight of heart in males (16) is 5.3 M8.4–11.5 g, in females (9), 4.5 M5.4–6.18 g; cardiac index is 7.25–M9.71–12.79. Length of intestine in males is 1635–M1806–2140 mm, in females, 1220 M1480–1690 mm (Altai). Number of caudal vertebrae in Tatariyan mink is 19–22.

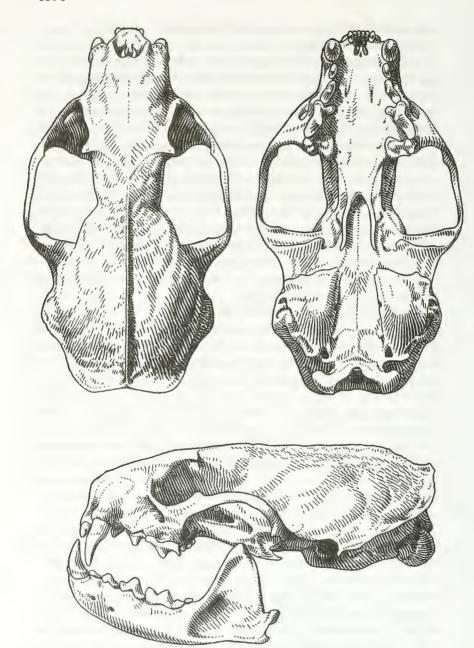


Fig. 351. Skull of American mink, Mustela (Mustela) vison Schreb.

928

Diploid number of chromosomes is 30.

Body length of males is 340-450 mm, of females, 310-375 mm; tail length of males is 156-247 mm, of females, 148-215 mm; length of hind foot in males is 51-70 mm, in females, 40-58 mm; length of ear in males is 20-29 mm, in females, 19-26 mm (in 110 males and females from Tatariya and 41 males and 31 females from Altai).

Weight of males in winter (Altai and Tatariya) is $500-1580~\mathrm{g}$, of females, $400-780~\mathrm{g}$.

Condylobasal length of male skull (32; Altai⁴) is 62.1–M66.4–72.6 mm, of females (14), 57.0–M59.3–61.6 mm; zygomatic width of males is 35.0–M37.1–41.4 mm, of females, 31.2–M32.8–34.4 mm; mastoid width of males is 30.3–M32.8–36.8 mm, of females, 27.6–M28.5–30.5 mm.

Os penis length (24) is 35.9–M40.5–45.4 mm. Weight is 0.110–M0.229–0.580 g. Age differences in dimensions and particularly weight of os penis are very significant. Length of bone in young (30; Tatariya) is 37.9–M41.7–45.2 mm, weight is 0.130–M0.167–0.210 g; in adults (30; Tatariya), length is 39.9–M44.6–49.7 mm, weight is 0.240–M0.336–0.450 g (V.A. Popov, 1943). Difference in weight is double.

Sexual dimorphism in body measurements and weight is very significant. Measurements of females (Tatariya) constitute 82–85% on average of measurements of males, while weight is 60–80%. Weight is very strongly variable according to season, reaching its maximum in autumn. At that time, males in Tatariya weigh about 1000 g, maximum 1580 g, females about 600 g, maximum 780 g. Least weight of males happens from April to June, females from June to August (nursing young). Average weight of the animals, and in part measurements, obviously change by year (V.H.).

Systematic Position

According to morphological characteristics, the American mink is closest to the European. These concern its main ecological and ethological characteristics. Some authors (among the most recent examples, K. Zimmermann, 1959; Gaffrey, 1961) even consider it as only a subspecies of the European, and suggest (Gaffrey, 1961), that in Middle Europe, remaining natural populations of the

⁴For skull dimensions of Tatariyan mink, see section "Geographic Variation"

European mink disappears (extirpated) due to its hybridization with the American, dissolving it so to speak, into the population of the latter.

According to our data, however, uniting the two minks into one species, cannot be accepted. They are close ("paired"), but independent species. This is indicated not only by their morphological, and most of all, craniological, characteristics (color-white marks on lips, a feature which is not very stable), but also by the absence of hybridization in nature here, in part a result of asynchrony of the reproductive cycles. It is possible that there is also a lack of compatibility in genital systems also occurs (see structure and size of os penis). Sharp antagonism exists in nature between these species—not only competition, in which the larger and stronger M. (M.) vison crowds out the European mink, usually simply destroying it (V. Popov, 1949; V. Popov et al., 1954).

Accurate material data on hybridization of the two mink species in nature are absent, apparently not only in our country, where this question was especially studied, but also in Central Europe. Their experimental crossing in captivity was also unsuccessful (Schmidt, 1933; V. Popov, 1949). At the same time, the Russian mink yields hybrids with the black polecat [M. putorius] (see above and below).

The American mink itself represents a sort of further development of the European mink—a further stage in the specialization towards predatoriness. This is indicated by the structure of its skull, with constricted interzygomatic area of braincase, more strongly developed protuberances and crests of skull, stronger dentition, etc. In comparison with the skull of the American mink, the skull of the European bears several infantile features.

The "paired" mink species show a quite remarkable parallelism with the "paired" species of polecats—black M. (P.) putorius and white M. (P.) eversmanni. The European mink corresponds to the first, and the American—to the second. This parallelism is manifested in a series of features—first of all, in skull structure and its interzygomatic region, relatively wide in the less specialized black polecat and constricted in the white. Features of parallelism in skulls of polecats with both pairs of "mink-polecat" are, however, developed at a higher level of specialization-mink do not attain such a height as each corresponding polecat species.

This is the parallelism of a pair of terrestrial species, in part of

929

even desert-steppe species [polecats], and a pair of species associated with the aquatic environment. In this situation, the level of specialization found in the polecat cannot be attained, possibly related to smaller and weaker prey [of mink].

The significant quantity of shared characters with polecats, on the one hand (especially American mink) and on the other—with kolonok does not allow us to split off mink as a separate subgenus, much less a separate genus, and also separate polecats ("Putorius") at a generic level from remaining species of genus Mustela. It is also hardly acceptable to separate mink from the genus Mustela and to unite them, as a subgenus, with an independent genus of polecats—Putorius (Stroganov, 1962). Mink serve as a connecting link between polecats and other species of the genus Mustela, especially the pair European mink—black polecat. They also produce hybrids. The American mink itself represents a branch of this trunk, with white polecat—its summit. (V.H.).

Geographic Distribution

Beginning with 1933, the American mink, usually in fairly large groups, were introduced into very different parts of our country, both in its European part, in Siberia, in the Far East, and also in the Caucasus. At the start, captive mink from fur farms were introduced, but quickly for further establishment, wild animals from populations naturalized to various places, began to be used, in particular, in the Altai. After the first years, introduction of animals within the range of Russian mink was stopped, or almost stopped, and new groups of mink were directed mainly into Siberia and the Far East where the Russian mink is absent. At the beginning of the 60's, and still earlier in some places (Altai), fairly considerable areas occupied by American mink were formed. However, in the majority of cases they were isolated from each other and one continuous range of this species is still absent in our country. There is a basis for considering that, on account of the new introductions and the natural dispersal, it will spread over time, although some territories are poorly suited as habitat for this species.

As a result of absence of sufficient data on distribution of the mink in separate locales, we will tabulate below only districts where it was introduced, irrespective of how many times and in which parts of these regions the animals were introduced. Also, intraregional distribution of local populations is not considered.

Starting in 1933, American minks were introduced into the European part of the USSR in Voronezh district (first experiment—Voronezh preserve). From 1933 to the beginning of 1963, the mink was introduced in various quantities to Murmansk and Arkhangel'sk districts, Karelia, in Kalininsk, Gork'ovsk, Volgogradsk, Chelyabinsk and Voronezhsk districts, and into Tatarsk, Bashkirsk, Mariisk as well as Lithuanian and Byelorussian Republics. Beyond the Urals, animals were introduced in Sverdlovsk, Tyumensk, Omsk, Kemerovsk, Novosibirsk, Chitinsk and Irkutsk districts, in Altai and Krasnoyarsk territories, in Tuvinsk, Buryatsk, and Yakutsk Autonomous Republics, into Magadansk, Kamchatsk and Amursk districts, into Khabarovsk and Primorsk territories, into Chukotsk national regions and in several other places, among them Sakhalin and Urup Island in the Kurils.

In the Caucasus, introductions were in northern Osetiya, in Georgia and Azerbaijan, and in Middle Asia—in the Tien Shan on territory of Kirgiziya.

The most northerly place of introduction—Kola Peninsula, lower Severnaya Dvina, mouth of Ob' River, mouth of Nizhnaya Tunguska, Podkamennaya Tunguska (middle course), Vilyui, upper Kolyma and lower Anadyr'. In the expanse between the Pacific Ocean and upper and middle courses of the Ob', mink are established generally southward, extending or almost extending to the state border. In western Siberia and in the European part of country, it extends southwards to the steppe zone. On the whole the range is not continuous, and separate places of introduction and separate regions of acclimatization, one may say are still isolated from each other, in some places by great distances. Regions of introduction in the Caucasus and Middle Asia are particularly remote from other places.⁵

In a series of places, small groups of animals were introduced in a few spots. These introductions have not yet given results in the sense of creating sufficiently significant populations from the perspective of being considered permanent. This applies to the

⁵Materials used in the construction of the map and the considerations given were obtained from the Main Board of Game Farm, of the Council of Ministers of RSFSR (Chief N.B. Eliseev; L.S. Tamantseva). Some data were obtained from V.A. Popov and G.A. Voronov).

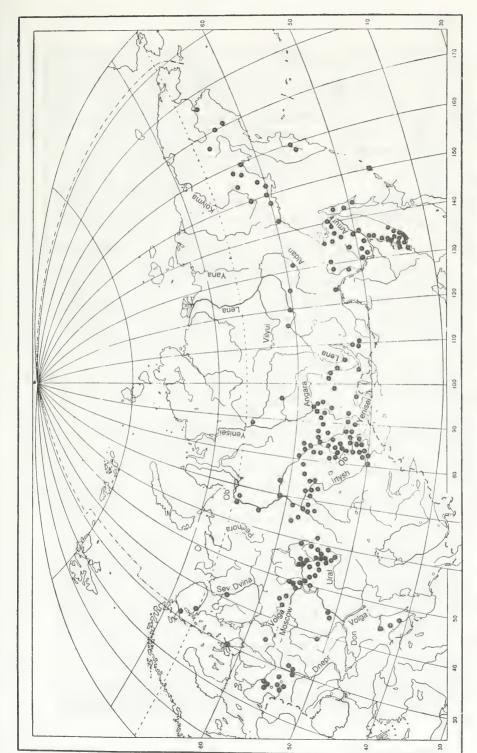


Fig. 352. Localities of introduction of American mink, Mustela (Mustela) vison Schreb. in the USSR. V.G. Heptner.



931 Fig. 353. Natural species distribution area of the American mink, *Mustela (Mustela)* vison Schreb. (from Hall and Kelson, 1959).

Extreme North, northwestern and in part western parts of the European USSR, as well as the Caucasus and Middle Asia. More positive results were apparently obtained in Byelorussia. Quite complete and numerous populations were created in the eastern European territories of the country—in Tatariya, in part in Bashkiriya and other adjacent places. Here populations are of exploitable number and density. Everywhere, in regions of habitation of the indigenous mink, *i.e.* to the west of the Ural, the American mink has crowded out and exterminated it.

In Siberia and the Far East, where in several districts living conditions are favorable for the introduced species, two quite sig-

nificant populations, both in numbers and in territory occupied, already have spread out. One occupies the Ussuri territory, including Priamur'e, and the other—Altai and adjacent places. In Trans-Urals (western Siberian lowland) where living conditions are less favorable for the American mink, numerous attempted introductions did not succeed. It is evident that a significant number of introductions into Siberia, in particular in the Extreme North and northwest, did not lead to the formation of stable and entirely naturalized populations.

Geographic Range outside the Soviet Union (natural).

The mink occupies the greater part of North America. The northern border extends along the northern shore of the continent, excluding, however, the Ungava Peninsula. Moreover, in the expanse from Hudson Bay to Amundsen Gulf in the Arctic Ocean, the northern border extends approximately along the southern limit of the tundra from Eskimo Point at Hudson Bay to its intersection of the northern coast of the continent at 125° west long.

The western border is formed by the Pacific Coast southwards to San Francisco and the eastern—by the Atlantic Coast, except the eastern extremity of the Nova Scotia peninsula. The southern border extends along the coast of the Gulf of Mexico, approximately to Corpus Christi, and thence is directed along an irregular line across the states of Texas, New Mexico Utah, Nevada and northern California passes to the Pacific Ocean. Mink are absent on the Aleutian and other islands of the Bering Sea, on Kodiak, on the Queen Charlotte islands and several other small islands along the Pacific Coast of America. In the east, the mink is absent in Newfoundland and the islands of the Gulf of Saint Lawrence.

In Europe the acclimatized mink is found in France, in Central Europe (F[ederal] R[epublic] G[ermany] and the G[erman] D[emocratic] R[epublic]), is widely distributed in the Scandinavian Peninsula. In Cent[ral] and in part in west[ern] Europe, it has replaced and destroyed the European mink (V.H.).

Geographic Variation

Very many geographic forms of mink have been described from the natural range in North America. Recent authors accept 14 races of the species *M. vison*, and moreover, a separate species *M. macrodon* extinct (exterminated) about 1860 and inhabiting, apparently, an extremely limited territory in the northeastern United States (New Brunswick and state of Maine). The actual number of races of the species in America, apparently, is less, and *M. macrodon*—differing only in somewhat larger dimensions hardly deserves to be split off as a separate species.

In the beginning, the various parts of our country were settled by captive-born mink from various large fur farms. The greater part of the material consisted of animals born in captivity in our farms. Animals directly imported from outside our borders constituted only a minority. The origin, *i.e.* the races to which this material belonged, even if we assume that at least a part of them were wild mink, is unknown. However, they were all, apparently, captives. Later, introduction of mink in the USSR proceeded by means of animals captured by us from the wild.

During study of the results of acclimatization, several real characteristics of the Tatarsk and Altaisk mink were established, and separate subspecies were described—tatarica and altaica (see synonymy). Difference between both "forms" lies in dimensions (tatarica is larger) and degree of development of white marks (in altaica, they are more, and may even appear on upper lip) and density of pelage (in altaica, it is slightly denser). The relationship of these "forms" to American mink is unclear.

The separation of the mentioned "subspecies" has no basis, in that what is signified by the word "form" does not correspond to the concept of subspecies. The word applies to very young populations, only yet being established from genetically heterogenous material (tatarica—mainly from Pushkino near Moscow, 1934; altaica—Kola fur farm, 1937). At the time of their study, they had existed in all for 14–15 years. Both populations themselves bore features of their "domestic" origin, in the form of occasional mutations that are unknown in wild mink, or are extremely rare (albinism, variant of underfur color, "scorched").

From published material (V. Popov, 1949; Ternovskii, 1958) it is clear that populations were subjected to the action of intensive selection and were rapidly changed—general dimensions and skull measurement changed, as well as frequency of occurrence and size of white marks, etc. All of this is entirely natural for animal groups with a heredity "uncoupled" during cage raising; it cannot be used

as a basis to accept the above-mentioned populations as established geographic races in the present sense of this word. One can only speak about differences in these artificially created populations. In the meantime, it is entirely unclear how they will form themselves, even after several decades, especially in case of union of ranges, not to mention the time needed for elaboration of actual subspecies.

Dimensions of mink from Tatariya (110 males and females) at the end of the 1940's (V. Popov, 1949), and from the Altai (41 males and 31 females), at beginning of the 50's (Ternovskii, 1958) are the following: body length of males from Tatariya is 375–M417–450 mm, of females, 330–M358–371 mm; the same from Altai—of males is 340–M395–450 mm, of females, 310–M345–375 mm; tail length of males from Tatariya is 195–M224–247 mm, of females, 178–M195–215 mm; tail length of males from Altai is 156–M184–205 mm, of females, 148–M158–173 mm; length of hind foot of males from Tatariya is 61.0–M65.0–70.0 mm, of females, 50.0–M54.5–58.0 mm; the same of males from Altai is 51–M60–67, of females, 40–M50–55 mm; length of ear of males from Tatariya is 22–M26–29 mm, of females, 21.4–M22.8–26.0 mm; the same of males from Altai is 20–M22–25 mm, of females, 19–M21–23 mm.

Average measurements of mink skulls from Tatariya: condylobasal length of males (20) is 68.95 ± 0.47 mm, of females (19), 60.65 ± 0.31 mm; zygomatic width of males is 39.75 ± 0.40 mm, of females, 33.9 ± 0.23 mm; interorbital width of males is 15.38 ± 0.31 mm, of females, 13.2 ± 0.17 mm (for craniological data on Altai mink, see above in section "Description") (V.H.).

Biology

Population. From 1933 to 1948, about 4000 mink were introduced into the territory of the USSR, distributed on 50 sites in 22 oblasts. To 1964, the total population of animals introduced into the European part of the USSR exceeded 2000, and in Siberia and the Far East, 14000 (V. Popov, 1964).

Concerning the results of these introductions one may judge that in 1957–1959, in the RSFSR (excluding Yakutiya) from 26.8 to 35.7 thousand wild minks of both species were caught. Of this number, American minks did not exceed 20–25%; *i.e.*, the number



934 Fig. 354. Arkhara river—a place of introduction and occurrence of the American mink in Arkharinsk region of Amursk district. June 1956. Photograph by A.G. Pankrat'ev.

of American minks caught per year was from 5350–6450 to 7150–8925. Separate count of the yield of each species were not made; therefore, the ratio of their number in regions where both species existed can only be estimated very approximately. Moreover, at the present time, the figures on skin preparation reflect not just the population numbers of the species but the numbers of hunters, their skill, the time they spend in this trade, etc. Due to the strength of a series of causes, mink, in many districts, are hunted less than would be allowed by their population.

More than 80% of the American minks are obtained from Siberia and the Far East, mainly from the Altai, Krasnoyarsk and Khabarovsk territories. From a series of indirect data, it can be estimated that the total number of the American mink in our country apparently does not exceed 30–40 thousand.

Habitat. With respect to choice of habitat, there are no differences between the American and European mink. In Georgia, in the Alazan' valley (Ekvitimishvili, 1951), mink stations* are areas around forest creeks 1.0-1.5 m wide and 15-100 cm deep, with steep banks freezing only along the sides. In the Altai (Ternovskii, 1955), lands favorable for mink are rich in fish, and have a good network of spaces under the shallow ice. Banks are well protected, steep and covered with trees containing a large amount of fallen limbs and branches, good undergrowth, with an abundance of mouse-like rodents. There, 3-5 mink are usually found along 1 km of shore-line. Satisfactory lands can be distinguished from less favorable conditions for nesting and protection; banks are weakly forested and with poor cover. On one km of shore-line, only 1-2 mink are encountered in such an area. Unfavorable areas are poor in fish, or if rich, then there are no under-ice cavities and few open water areas. In one km of shore-line in these conditions, no more than one mink may be met with. Surroundings of the first and second types predominate in the lower courses of small rivers, and the third—in the upper reaches of rivers.

Food. Of greatest significance in foods of mink in Tatariya (V. Popov, 1941, 1949) are voles (36% occurrence), fish (28.8%), crustaceans (26.7%), frogs (17%) and aquatic insects (19.8%). Importance of each food changes noticeably according to season.

935 In winter, foods obtained from water prevail: fish (45.5%), crustaceans (32.2%) and frogs (17%); the percentage of voles decreases to 10%. In spring, the significance of terrestrial animals increases; occurrence of voles increases to 55.6%, of insects—to 20.7%, birds comprise 6% and occurrence of crustaceans decreases to 18%; in food remains, small hares are encountered. In summer, a greater diversity of food is characteristic. Vole occurrence is high (40.6%), crustaceans (30%), insects (29.6%), frogs (21.2%), birds (mainly in the form of nestling) and their eggs—16.7%. In autumn, voles occur in 50% of data, fish in 15.5–38.7%, and crustaceans in 22.4%.

Within the boundaries of montane Altai (Ternovskii, 1955), in the diet of the American mink, mammals constituted 58.5% (occurrence); rodents 53.8% (including voles 50.2%), and shrews and moles 4.7%. Birds were met with in 3.3%. Reptiles constituted 1.0%, amphibians—5.8%, fish—54.9%. Among birds, 11 different species were recorded—most frequently, dippers [Cinclus cinclus]

^{*}The Russian word is statsiya; stantsiya might have been meant—Sci. Ed.

and pine grosbeak [Pinicola enucleator]. Among fish, small ones prevail: minnow, gudgeon [Gobio gobio] and wide-headed sculpin [Cottocomephorus], in all, 11 species of the 26 species known in Altai. Mollusks constituted only 0.05%, insects 25.6% (mainly from stomachs of fishes). Here also (Berger, 1947), in the earlier period of acclimatization, the occurrence of insectivores in the food of American mink constituted 3.9%, hares—5.1%, squirrels—2.6%, mouse-like rodents 43.6%, water voles—14.1%, fish 7.7% and insects—10.2%.

In Sverdlovsk district (L.M. Tsetsevinskii), mouse-like rodents constituted—41.8% of mink food, water voles—25%, birds—12.5%, fish—20.9% and insects—12.5%. In Irkutsk district (Vladimirov, 1940), murid rodents constituted 20.5%, water voles—30.1%, birds—16.9%, fish—15.7%, amphibians—1.2%, and insects—14.4%.

In connection with differences in the composition of aquatic and bank fauna, a well-defined geographic variation is observed in the foods of American mink. The absence or scarcity of river crustaceans in many of the water bodies of our country is particularly evident. In the Far East, in the food of American mink, crustaceans are replaced by fresh-water amphipods which are eaten in great quantities (Yu.A. Salmin and V.D. Shamykin). In the first years after introduction of American mink, living for a series of generations on farms, food obtained on land predominated, but feeding characteristics quickly changed character, and approached that of wild mink in type.

In North America (V. Popov, 1949), warm-blooded animals have greater significance in the food of mink, than in the USSR (mouse-like rodents, muskrat).

The mink eats 4–9 times daily. The quantity of food eaten during this time constitutes 20–25% of the live weight of the animal. In Tatariya (V. Popov, 1949) and in the Altai, the American mink makes a store of food. The size of the store reaches 1200 g (6 frogs, 3 water voles, 1 tundra vole, 1 viper, 9 minnows and 1 wide-headed sculpin) (Ternovskii, 1955).

Home range. Dimensions of the home range of each individual is subject to seasonal change. In mink having a settled mode of life, area of the home range in southern Tatariya on average equaled about 16 hectares, fluctuating from 0.1 to 40.0 hectares (V. Popov, 1949). Dimensions of daily range of activity in winter fluctuate from 0.1 to 2.1 hectares. In summer, when food yield increases,



936 Fig. 355. Brood shelter of American mink. Arkhara river in Arkharinsk region, Amursk district. June 1956. Photograph by A.G. Pankrat'ev.

the home range decreases; usually only a small part of the range is exploited, sometimes, only a radius of 50–80 m from the burrow. In the Altai, in winter mink live in an area of 200–300 m, not wandering more than 100 m from the bank, and are confined to open water (polynia) (Ternovskii, 1955). In the Far East (N.M. Berger), 0.8–1.0 mink may patrol on 1 km of the shore-line, in eastern Siberia—0.3–1.0; in Krasnoyarsk territory—0.04–0.10; in Kuznetsk Alatau—0.7–0.8. In spring, the animals undertake movements along the river banks to a distance of up to 20–30 km; in autumn—up to 7–10 km.

In America (USA) in an area of 440 hectares (280 hectares of which is dry land), 17 minks were captured and tagged (14 males

and 3 females); 5 of them (29.4%) were caught a second time in the same winter. During the following 4 years (winters of 1945/48) in the same area, only 6 new minks were caught, out of which 2 were repeatedly caught (4 times). Males were considerably more active than females and the area of 440 hectares was insufficient for them; one male, in the course of three years moved on to the area every month, making a round trip of about 1.5 km in one and the same route and then returned. Females were less active—repeated hunting was achieved within a distance of from 25 to 400 m from the place of marking (McCabe, 1949).

Burrows and shelters. In the Volga-Kama territory, there are 4 types of burrows of American mink (V. Popov, 1949). They are constructed frequently in the hollows in root masses of growing trees, and rarely—in hollows of fallen ones. The holes are often in the root masses of hummocks ("koblakh")* of the alder which are typical for flood-land alder swamps. These holes are characterized by a large number of entrances and twisting passages. Rarer are earth holes of structure similar to that of the European mink. The number of exits of the mink burrow varies from 1 to 8. In the breeding burrow, exits are often stuffed with grass so young cannot crawl away. Usually, the breeding burrows are situated not more than 20 m from the bank of the water body. Burrows of single animals are also encountered (considerably more rarely) at a distance of up to 50-60 m. The bedding of the nesting chamber consists of dry grass and leaves, wool and underfur of consumed animals and wood dust.

Out of 24 mink shelters investigated in the Altai (Ternovskii, 1955), 54% were found in hollows of fallen trees, 34%—in intraroot hollows among the roots of trees, 4%—in hummocks and 4%—in openings among rocks and soil layers. Mink shelters, in the latter case, are found in sections of floodlands which are not submerged with water, at 2–10 m from the water level, but no more than 50 m from it. The bedding in the nesting chamber usually consists of sedge, *Carex pediformis* ("puzzle grass").

Daily activity and behavior. The mink is active at various times of day. The rhythm of diel activity changes in different seasons in relation to security of food, prevailing means of obtaining it, weather conditions, etc. Thus, in the rut period, animals are highly active

^{*}Local word?-Sci. Ed.

throughout entire 24 hr period. For the period of pregnancy, daily activity typically shows two peaks. In the period of nursing young, the female is active most of the 24 hr period. In summer, the litters are active mainly at twilight. Later in autumn, the activity during the day light hours again increases (Ternovskii, 1955).

In Tatariya, in American mink in winter (January) three periods of activity are observed with an interval between the peaks of approximately 8 hours (V. Popov, 1949). The first—a daylight period, lasts from 10 until 14 hr and is associated with obtaining food in water bodies. The second—at twilight, begins at 18 hr, somewhat before nightfall. The third occurs in the second half of the night and the pre-dawn period. During severe frosts, activity decreases. The mink is maximally active in July–September, and minimally in November–February. Males are more active in March and less—from the end of rut until August. Females are maximally active in July–September. In winter, in a 24-hr period, the mink moves from some tens of meters to 4–5 kilometers.

In the Altai, the mink is most active morning and evening, and also at the end of the night (Ternovskii, 1955). In winter and summer, activity is less than in autumn and spring. Rut and dispersion occur in spring, and in autumn, dispersion of young and adults, searching for home ranges, and then mink are maximally active. In cloudy calm weather, activity grows. In winter, with air temperature from -20 to -37°C, the mink is active for not more than 51-64 minutes during the 24 hr period. In December-January, it leads a hidden, subnival mode of life. If in October and the first half of November, the length of the 24 hr trail reaches 800-1000 m, then during the period of deep snow, the daily trail decreases by 3-6 times and does not exceed 100 m.

During swimming, undulating movements of the trunk play the main role. The swimming web is no more developed than in ermine, weasel and kolonok. In warm water (24°C), mink can swim for more than 3 hours without stopping. In cold water, animals died within 27 min. During this time, body temperature fell from 40°C to 19–20°C. With water temperature up to 8°C, the body of the mink cooled down under water for 118 minutes, while in ermine and forest polecat—in 26–28 minutes (Ternovskii, 1955).*

Seasonal migrations and transgressions. In winter, the character of activity in mink depends upon the abundance of food and its

^{*}The mink body is better insulated in water—Sci. Ed.



938 Fig. 356. Tracks of American mink on fresh new-fallen snow. Fudzin river, western slope of Sikhote-Alin'. December 1956 (Photograph by A.G. Pankrat'ev).

availability. Complete freezing of water bodies, absence or small number of polynias,* air holes and other opportunities to penetrate under ice call forth emigrations and sometimes considerable concentrations of mink in those places where food is more abundant and available. In areas of the meadow type with little food, some minks lead a migratory mode of life, performing movements of 2–3 or up to 4–5 km in a 24-hr period in an area of floodland of up to 60 hectares (in the presence of abundant food, minks do not move away from the burrow more than 50–100 m). Migratory animals restrict themselves to one place for several days, and then perform a movement to settle down in a new place, again for several more days. Young mink, dispersing, also undertake migrations. More significant translocations were observed in the first period after introduction of mink, especially in cases of

^{*}Ice-free water surface-Sci. Ed.

unsuccessful choices of places. Mink moved from the introduction site a distance of 15 km (Tatariya) to 40-60 km in Siberia, and for a distance of up to 100-120 km in the Far East.

Reproduction. In our country, estrus in American mink proceeds from the end of February to the beginning of April. For the most part, mating takes place in mid-March (Kler, 1941); (V. Popov, 1941, 1949), i.e. a month earlier than Russian mink. Estrus in separate individuals lasts one month, with 6-8 day intervals. The percentage of fertilized females equals 95-100. Duration of pregnancy is 51.3 days on average, fluctuating from 40 to 65 days (Kler, 1941). Differences depends on duration of the latent period in embryonic development, which lasts from 2-3 weeks to 1 month. After formation of the placenta, development goes on for 25-26 days. Embryonic mortality is great and reaches 60-70%. It is most of all determined by magnitude of litter and depends upon external conditions of environment which control condition of the female organism. Birth takes place during the period from 4 to 22 May.

In the Altai, the first signs of spermatogenesis were noticed in January. Already by 10–15 March, all stages of spermatogenesis, and sperm were in the tubules of the epididymis. On 1 February, pre-estrus proliferation of the uterus was observed in the female (Ternovskii, 1955). The first signs of rut were noticed at the end of February. It proceeded throughout March and the first half of April; peak of rut—the second ten days of March. Its general duration here is 45 days.

The number of young in the litter fluctuates from 1 to 9, and in exceptional cases, reaches 11 (Tatariya) and 16 (USA). In southern Tatariya, average litter size fluctuated in various years from 3.2 to 5.8 (V. Popov, 1941).

Growth, development and molt. Weight of new-borns fluctuates from 6 to 11 g. They are born blind, but develop rapidly, and eyes open at age of 30–31 days. Differences in increase in weight and dimensions between males and females are clearly noticeable only after 40 days.

The lactating period lasts for 2–2.5 months. Mink's milk contains 3.8% lipids, 6.2% protein, 4.6% sugar and 10.66% mineral salts. Already at the age of 20–25 days, young minks begin to try food brought by the mother. In autumn, they attain adult dimensions.

On farms, minks live 7-10 years, but are usually killed for their skins before reaching their age limit.

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The larger, stronger American mink ousts and depresses the European.

There are little data concerning population dynamics, and these data are not always reliable. The history of establishment of mink in the Altai gives some conception of growth rate of the transplanted populations. Acclimatization was started in 1937. In 1937–1941, 248 minks were introduced. During the period 1940–1953, 431 minks were transferred from one region to another, to accelerate the transplantation process. As a result, during a period of 19 years, the American mink settled in hundreds of rivers and streams and occupied a territory of 79,400 km². By the beginning of the 1960's, they numbered several thousands (Ternovskii, 1955).

Field characteristics. It is not always easy to distinguish between the tracks of American mink and European. Jumping with paired paw prints is a typical gait for the European mink. Length of the jump is 25–35 cm. In American mink, tracks on the snow most often form a group of 3–4 paw prints. Paired tracks and the unique pace forming a chain of tracks are rarely observed. Length of a jump is significantly greater—55–60 cm.

In the Altai, maximum jump length of the American mink is 1200 cm, while running, the mink can jump to a height of 50 cm. It can attain a speed of 20 km per hour for short distances; at a moderate walk—8-12 km, and in slow movement—3-5 km. The mink cannot run in loose snow deeper than 15 cm.

Tracks of the paws of males are always larger than females; the male track is equal to 4×3.5 cm on average, but the female track is 3.5×3.0 cm. While moving slowly, the length of the female jump is always shorter than the male. Sex can also be determined by the characteristics of urination on the snow. The weight load on 1 cm² of foot surface is large, 15–31 g (average of 20 samples—20 g). Weak fur covering of the foot prevents snow freezing on it. "Sliding hills" and grooves in mink trails, as in otters, are explained by their need to dry the fur in winter after coming out of water (Tarnovskii, 1955).

Identification of tracks and burrows of mink may also be determined by contents of excrement and food remains near entrances to burrows (P.Yu.).

Practical Significance

Acclimatization of the American mink in the USSR achieved its colonization in water bodies where it was previously absent for some reason or where it was destroyed. The American mink, as an object of the fur trade, gives a larger and higher quality skin than the Russian mink and its settling in water bodies, mainly in montane regions of southern Siberia and Far East, may increase the commercial yield to us of valuable "colored" furs.

Trade in American mink in the USSR began in Tatariya in 1938. At the present time, the animal is mainly used for further settling by means of its capture in live traps.

In some parts of North America, the mink destroys muskrats in quite significant quantities, especially the young. There are analogous complaints in Siberia.

In past years, intensive breeding of the American mink in farms, both abroad and in the USSR, has pushed hunting of wild mink to a secondary position (P.Yu.).

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A

aberrans cf. Meles abyssinica cf. Mellivora admirata cf. Mustela adustus cf. Canis Aeluroidae 54 aestiva cf. Mustela Ailuridae 54 Ailurinae 911 Ailuropoda 54, 402, 907, 908, 909, 911 Ailuropodidae 54 Ailurus 54, 402, 907, 908, 909, 911 alhperakyi cf. Vormela Alopex 62, 63, 68, 99, 194, 194, 195, 196, 268 - beringensis 196, 207 beringianus, 196 — fuliginosus 208 - groenlandicus 208 - halensis 208 - innuitus 208 - lagopus 56, 63, 65, 195, 196, 196, 197, 199, 202, 205, 206, 207, 208

— ungava 208
alpinus cf. Mustela, Kolonokus
altaica cf. Mustela
Amblonyx 498, 853
— cinerea 853
americana cf. Martes
Amphicyoninae 62
Amphicynodontinae 62, 402
amurensis cf. Meles

- spitzbergenensis 196, 206, 208

pribilofensis 208semenovi 196, 207

anakuma cf. Meles Anurocuon 383 Anurocyon 383 - clamitans 383 Aonyx 492, 498, 854, 883 - capensis 853, 854 - cinerea 851, 853, 854 - hessica 883 Arcticonus 404 Arctocyonidae 54 Arctogale 636, 640 - erminea 663 - tobolica 663 Arctoidea 54 Arctonyx 493, 498, 817 arctos cf. Ursus arenarius cf. Meles Artiodactyla 10, 11, 54 asiatica cf. Martes aureus cf. Canis. Mustela aurobrunnea cf. Lutra australis cf. Dusicyon, Mustela

В

baicalensis cf. Ursus barang cf. Lutra Bassariscus 69, 907, 908, 911 Bassaricyon 911 beringiana cf. Ursus beringianus cf. Ursus birulai cf. Mustela, Kolonokus boccamela cf. Mustela Borophaginae 62 bosniaca cf. Martes brachyura cf. Martes

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¹Page numbers with description are given in bold and those with illustrations, in italics.

	Broiliana 817	— hodophylax 145
	brokmani cf. Mellivora	— hungaricus 108
		— indicus 108
	С	— italicus 145
		- kamtschaticus 124, 136
	Constant in a	- kurjak 145
	Caenolestoidea 9	lagopus 194, 196
	canescens cf. Meles	— laniger 123, 141
	Conepatus 498	lanka 108
	Canidae 54, 55, 57, 58, 60, 61, 62, 69, 272,	— latrans 63, 100
	402, 907, 911	— lepturus 383
	Caninae 62, 63, 66	— lupaster 108
	Canis 53, 62, 63, 68, 96 , 96, 98, 99, 132,	lupus 56, 59, 63, 64 , 96 , 97, 100, 123 ,
	194, 268	123, 124, <i>125</i> , <i>129</i> , 132, <i>133</i> , <i>135</i> , 136 ,
	— adustus 63, 99	137, 137, 138, 139, 139, 140, 141, 141,
	— albus 123, 136	142 , 142, 143 , 145, 146
	— altaicus 139 , 139, 142	— lycaon 146
	— alopex 318	— mackenzii 145
	— algirensis 108	— manningi 137, 146
	— alpinus 63, 383, 386	— marocanus 108
	— arabs 145	— melanotus 319
	— argunensis 124, 142	— mesomelas 63, 99, 108
	— arundinaceus 123, 139	— minor 108
	— aureus 63, 64, 96, 100 , 100, 101, 102,	— montana 319
	<i>105</i> , <i>107</i> , 108 , 108	— moreotica 100, 108
	— australis 63	— naria 108
	— australis = antarcticus 53	niger 97, 99, 146
	— bactrianus 141	— orientalis 124
	— baileyi 146	— pallipes 123, 141, 145
	— beringiana 319	— pambasileus 145
	— bernardi 137, 146	— primaevus 383
	— campestris 123, 139 , 140, 142	— procyonoides 69
	— caragan 318	— rex 124, 143
	— caucasica 100	— rufus 146
	— caucasicus 108	— schensi 53
	— chanco 123, 141 , 142	— simensis 63
	— communis 123, 137	— soudanicus 108
	— coreanus 124	— signatus 145
	— corsac 265	— syriacus 108
	— crucigara 319	typicus 100, 108
	— cruesemanni 108	— tschiliensis 142, 145
	— cubanensis 124, 140	— tundrarum 146
	— deitanus 145	— turuchanensis 124, 136
	— desertorum 123, 141 , 142	— vulpes 265, 318, 319
	— dingo 52, 53, 61, 98, 99	Canoidea 54, 55, 58, 402, 497, 498, 907 ,
	— dorogostaiskii 124, 142	911
	- dukhunensis 383	caparioccoi cf. Mustela
	— dybowskii 124, 136	capensis cf. Mellivora
991	— ecsedensis 108	Capreolus capreolus 837
	— familiaris 53, 56 , 96, 100	Carnivora 10, 11, 49, 52, 53, 60, 907
	— gregoryi 146	caucasica cf. Mustela
	— hajastanicus 124, 140	caucasicus cf. Meles, Ursus
	hattai 124, 143	cavifrons cf. Ursus

- dinniki cf. Ursus Cetacea 10, 11 Cephalogale 402 desertorum - pallipes cf. Canis Cervus elaphus 837 Dinocyon 402 chamus cf. Fennecus Diprotodontia 9 chanco cf. Canis dolichocrania cf. Vulpes Charronia 498, 502, 505, 508, 604 Dugong 17, 23, 24 - dugong 20, 21, 24 chinensis cf. Lutra Dugongidae 17, 23, 24 Chiroptera 10, 11 Dusicyon 62, 68, 268 Chrysaeus 383 Chrysocyon 62 - australis 63 - brachyurus 59, 62, 63 - cinereo-argentatus 63, 67 cinerea cf. Amblonyx - culpaeus 63 cinereo-argentatus cf. Dusicyon - hagenbecki 63 Clethrionomys rufocanus 521 - rutilus 521 E collaris cf. Ursus colore griseo cf. Vulpes ecsedensis cf. Canis Conepatus 493, 498 Edentata 10 consica cf. Mellivora Eira 498 coreana cf. Mustela Embrithopoda 23 coreensis cf. Martes Enhydra 50, 492, 493, 498, 499, 854, 882, Creodonta 54 882, 883 crucigera cf. Vulpes - gracilis 895 culpaeus cf. Dusicyon - kamtschatica 884, 895 Cuon 60, 62, 63, 383, 383, 384, 386 - lutris 854, 863, 883, 884, 885, 889, 891, -- adustus 392 **894**, 894, **895** - alpinus 60, 63, 384, 385, **386**, 386, 388, - marina 894 390, **391**, **392**, 392 - nereis 895 - dukhuneusis 392 - orientalis 895 - fumosus 392 - reevi 883 - hesperius 392 - stelleri 895 - infuscus 392 Enhydriodon 854 - jason 386, 392 Enhydris 882 iavanicus 386, 392 992 Eomellivora 803 - laniger 392 Eotheroides 24 - lepturus 392 Euarctos 403, 404, 406 - primaevus 392 Eumetopias 53 - sumatrensis 392 Eumustela 637 Cuoninae 62 Euprocyon 912 cylipena cf. Mustela Eutheria 10 Cynalopex 265 euxina cf. Vormela Cynarctinae 911 eversmanni cf. Mustela Cynodictis 60 Еуга 493 Cynodon 402 Cynodontidae 402 Cynaonyx 854 Felidae 54, 55, 57 D Felis catus 56 - libyca 56 Dermoptera 10 - manul 50 Desmostyliformes 23 - sylvestris 56 desertorum cf. Canis

Feloidea 54, 55, 497 Н Fennecus 62, 68, 268 - chamus 63 hagenbecki cf. Dusicvon Halicore 25 - pallidus 63 - rüppeli 63 Halitheriinae 23 - zerda 59 Halyanassa 42 zerdus 63 hamgyensis cf. Martes Ferae 10, 49 Helarctos 397, 398, 400, 403 ferghanae cf. Mustela — malayanus 403, 483 Ferungulata 10, 54 Helictis 493, 498, 817 Fissipedia 53, 54, 60 heptneri cf. Meles, Mustela flavescens cf. Vulpes Herpestes auropunctatus 52 Foetorius 636 - javanicus 52 - foetorius 745 hoole cf. Vulpes foina cf. Martes huli cf. Vulpes fontanieri cf. Mustela hungarica cf. Mustela formosanus cf. Ursus hungaricus cf. Canis fuliginosus cf. Alopex Hyaenidae 54, 55, 57, 60 Hyaenodontidae 54 Hyracoidea 10, 22, 54 G Hydrictis 853 Hydrodamalidae 17, 23, 24, 25 Gale 636 Hydrodamalis 18, 23, 25, 25 Galictis 493, 498 - gigas 25, 27 gedrosianus cf. Ursus - stelleri 25 Glires 10 Hydromustela 637 glogeri cf. Mustela Grammogale 498 gregoryi cf. Canis griffithi cf. Vulpes Ictis 636 Grisonella 498 - boccamela 644 groenlandicus cf. Alopex, Ursus kamtschatica 644 Gulo 493, 498, 500, 501, 614, 614, 616, - nikolskii 644 617, 641, 803 - nivalis 644 - albus 629 Ictonyx 498, 783 - arcticus 618, 628 inaurita cf. Mellivora — arctos 618, 628 indica cf. Mellivora — biedermanni 618, 628 indochinensis cf. Martes — borealis 618, 628 mesomelas cf. Canis - gulo 58, 617, **618**, 618, 619, 622, 624, Insectivora 10, 11, 54 **628**, 628, **629**, 629 isabellinus-syriacus cf. Lutra - kamtschaticus 618, 629 itatsi cf. Mustela katschemakensis 629 intermedia cf. Martes, Vormela — luscus 618, 629 — luteus 629 J schlosseri 616, 618 - sibiricus 615, 618, **628** japonicus cf. Ursus - vancouverensis 629 jessoensis cf. Ursus — vulgaris 618, 628 - wachei 618, 628 Guloninae 641 gwatkinsi cf. Martes kalmykorum cf. Vulpes gyas cf. Ursus katschemakensis cf. Gulo

Kolonokus 673, 640, 690, 691, 723 — alpinus 664, 686

— australis 700 — birulai 664, 686 — coreanus 700

— raddei 686 — sibiricus 700

kolymensis cf. Ursus koreana cf. Martes

koshevnikovi cf. Vormela kuatunensis cf. Martes

kutab cf. Lutra

993 L

labradorensis cf. Ursus Lagomorpha 10, 11 Lamprogale 502, 604 laniger cf. Ursus, Lupus larvata cf. Mustela lasiotus cf. Ursus Latax 882 Leptarctinae 497 Leptonyx 785

leptorhynchus cf. Meles Leucocyon 194

leuconota cf. Mellivora leuconyx cf. Ursus leucurus cf. Meles libyca cf. Poecilictis

lineiventer cf. Mustela

Lupulella 99 Lupus 96

— altaicus 124 — filchneri 124

karanorensis 124laniger 123

— tschiliensis 124 luscus cf. Gulo luteus cf. Gulo

Lutra 493, 498, 500, 500, 501, 851, 851, 852, 853, 854, 854, 882, 883

--- amurensis 855, **867**

angustifrons 868annectens 853

— aurobrunnea 855, 869

aurobrunnea 855, 869baicalensis 855, 867

barang 866, 869canadensis 853

— chinensis 868

— enudris 853

- felina 853

- gracilis 884

- isabellinus-syriacus 868

- incarum 853

- kamtschatica 855, 867

- kutab 855, 869

— lutra 853, 854, 855, 856, 858, 859, 862, 865, 866, 866, 867, 868, 869

maculicollis 853marina 884meridionalis 867

minor 718mira 853

- monticola 855, 868

nair 865, 869
nudipes 854
oxiana 855, 867
perspicillata 853, 865
platensis 853

platensis 853
provocax 853
seistanica 855, 867
stejnegeri 855, 867
stelleri 884
sumatrana 853

— vulgaris 854, 855, **867**Lutreola 636, 640, 727

altaica 924
borealis 719
europaea 718
lutreola 719
vison 924

Lutrinae 497, 498, 817, 851, 853

Lutrogale 498, 853

Lutronectes whitelyi 855, 863

Lycalopex 62, 68

— microtis 62

— thous 62

Lycaon 58, 60, 62, 63, 386

microtis 63
pictus 59, 60, 63
thous 63
Lycaoninae 62
lymani cf. Mustela
Lyncodon 493, 498

M

mackenzii cf. Canis Mammalia 10 Manati balaenurus 25 — gigas 25

manchurica cf. Mustela mandchuricus cf. Ursus

- melli 611

marinus cf. Ursus - milleri 598 maritimus cf. Ursus - nehringi 587, **597** Marsupialia 10 - notialis 596 Martes 493, 498, 501, 501, 502, 502, 503, obscura 508, 532 504, 505, **507**, 516, 590, 595, 615, 616, - ochracea 507 637, 641 — ognevi 585, 597 - abietum 553, 568 — pennanti 503, 505, 516, 590 - alba 507, 596 - peninsularis 611 - altaica 508, 530, 585, 597 — princeps 531 - americana 504, 505, 516, 590 — rosanovi 585, 587, 596 angarensis 508, 531 — ruthena 553, 586 — arsenjevi 508, 532 --- saba 611 — asiatica 507 — sabaneevi 553, 568 - aterrima 610 - sahalinensis 508, 532 — averini 530, 580 - schantaricus 532 baicalensis 531 - sajanensis 508, 531 --- brachyura 533, 533 - sylvatica 568 — borealis 553, 568 - sylvestris 568 - bosnica 585, 598 - svriaca 598 - brachyura 532 - szetchuensis 611 - bunites 598 — tomensis 508, **530** - chrysospila 611 — toufoeus 598 - coreensis 508 - szetchuensis 611 - domestica 502, 596 - tsuensis 533 - fagorum 596 - tungussensis 508, 531 - ferruginea 507 - uralensis 553, 569 — flavigula 503, 505, 506, 590, **604**, 605, vitimensis 508, 532 607, 609, 610, 610, 611 - vulgaris 553 — foina 505, 506, 506, 507, 585, 586, 587, — yeniseensis 508 589, 593, **596**, **597**, 598, 602 yuenshanensis 611 - fusco-flavescens 507 - zibellina 501, 505, 506, 506, 507, 507, gwatkinsii 505, 611 508, 513, 518, 523, 528, 530, 531, 532, - hamgyensis 508 **533**, 533 ilimpiensis 508, 531 Martinae 505, 541 - indochinensis 611 Megalotis 268 - intermedia 597 Melodon 817 iacutensis 508, 532 Melanarctos 404 jeniseensis 531 — cavifrons 404, 408 kamtschadalica 533 Meledes 816 — kamtchatica 533 — leptorhynchus 816 - koreana 611 Meles 493, 494, 498, 500, 500, 803, 816, — koreensis 533 817, 818, 818 - kozlovi 598 — aberrans 819, 833 - kuatunensis 611 - altaicus 819, 833 — latinorum 569 - amurensis 817, 819, 836, 837 - leucolachnea 597 — anakuma 817, 819, 836, 837 -- lorenzi 553, 569 - arcalus 817, 837 - martes 505, 506, 507, 517, 553, 553, --- arenarius 818, 819, **834**, 835 554, 557, 562, 563, 567, **568**, **569**, 569 — atavus 818 - maculata 507 - blanfordi 819, 837 - mediterranea 598 — canescens 819, 833, 836, 837 994 — melampus 505, 533 — caucasicus 819, 832

— danicus 837

Mesaxonia 10 Meles europaeus 819 Mesonychidae 54 - gennevauxi 818 - heptneri 819, 832 Metatheria 10 Miacidae 54 - leptorhynchus 819, 830, 833, 837 — leucurus 817, 837 Miacoidea 54 — marianensis 837 michnoi cf. Mustela - melanogenys 819, 837 Microaonyx 853 - meles 493, 817, 818, 818, **819**, 819, 820, microdon cf. Paraonyx 823, 826, 830, **832**, **833**, 833, **834**, **835**, middendorffii cf. Ursus 835, 836, 836, 837 macrotis cf. Lycalopex - minor 819, 833 minor cf. Canis minuta cf. Mustela - ponticus 819, 837 - raddei 819 Miosireniae 23 - rhodius 837 mongolica cf. Mustela -- schrenkii 819, 836 Monotremata 10 — severzovi 819, 833, 833, 835 montanus cf. Vulpes - sibiricus 819, 833 monticola cf. Lutra, Vulpes - talassicus 819, 835, 836 moreotica cf. Canis - tauricus 819, 832 mosanensis cf. Mustela - taxipater 818 mupinensis cf. Ursus - taxus 819 Mustela 493, 498, 501, 505, 639, 636, 636, — thordi 818 641, 643, 848, 690, 691, 704, 705, 723, tianschanensis 819, 835, 836 724, 781, 783, 787, 929 - typicus 819 — aestiva 663, 673 meles cf. Meles - admirata 774 Melinae 498, 802, 803, 816, 851, 854, - alascensis 677 Melogale 498, 817 - alba 585 melli cf. Martes - albica 719, 731 Mellivora 493, 498, 499, 500, 801, 801, - algirica 671, 676 802, 802, 803 - alleghaniensis 657 - abyssinica 812 - alpina 696 - broekmani 812 — alpinus 691 Mellivora buchanani 812 995 — altaica **641**, 643, 648, **686**, 686, 689, - capensis **804**, 804, 805, 807, 809, **812**, 690, 692, 694, 695, 696, 697, 697 812 — amurensis 508, 773 -consica 812 - angliae 749 - cottoni 812 - anguinae 676 - inaurita 812 - arctica 675, 675, 676 - indica 812 — asaii 712 - leuconota 812 - asiatica 507 - makwelli 812 — astutus 697 - pumilio 812 - aterrima 604 — ratel 804 --- aurea 771 -- signata 812 - aureola 749 - sigulata 812 - aureus 748, 770 - vernayi 812 - australis 710 — wilsoni 804, 812 - baicalensis 508 Mellivorinae 498, 803 balkarica 664, 673 Melursus 50, 399, 403 — bangsi 676 — ursinus 403, 483 - baturini 664, 675 Mephitinae 498, 803 - biedermanni 732 Mephitis 493, 498

— binominata 719, 730

- birulai 664, **674**, 695

meridionalis cf. Lutra, Ursus

- invicta 677

Mustela boccamela 644, 650, 654 - itatsi 700, 706, 711 --- borealis 553, 604, 719, 730 — kadiacensis 676 - brachyura 507 kamtschatica 508, 652, 675 — budina 719, 731 - kaneii 663, 675 - caledoniae 749 - kanei 675 - campestris 657 — karaftensis 644, 652 — canigula 712 - karaginensis 664, 675 - caparioccoi 697 — katian 641, 690, 697 caucasica 655, 730 — kerulenica 644, 653 — caucasicus 719 - koreensis 508 - celenda 677 - larvata 770, 773 - charbinensis 701, 712 leucolachnea 585 - cicognanii 679 - lineiventer 754, 772 - longstaffi 686, 697 - coreana 712 - cylipena 718, 731 - lutra 854 - davidiana 712 - lutreola 637, 641, 643, 691, 718, 718, - dauricus 772 719, 720, 722, 726, 728, 729, 730, 731, - digna 664, 675 731, 732, 924, 925 - dinniki 655 - lutris 882, 884 - dombrowskii 644 — lymani 667, 674, 676 — domestica 585 — macrodon 932 — erminea 636, 637, 641, 642, 648, **663**, — manchurica 700, 710, 711, 712 663, 664, 665, 666, 669, 671, 672, 673, -- martes 553, 585 **674**, 674, 675, **676**, 676, 677, 737 martinoi 664, 674 — eskimo 657 - melampus 507 — eversmanni 638, 640, 641, 642, 705, - michnoi 772 719, 742, 743, 744, 753, 753, 754, 755, - miles 700, 710 758, 760, 761, 763, 768, 771, 772, 773, — minima 676 774, 781, 929 - minor 729 - fagorum 585 — minuta 650 - fallenda 677 - mongolica 677 - ferghanae 674, 676 — mosanensis 644, 657 — flavigula 502, 533, 604, 719 mosquensis 737, 749 - foetidus 749 - moupinensis 712 — foina 585, 587 - murica 676 — fontanieri 712 — namiyei 644, 652, 657 — frenata 640, 641 naumovi 664, 675 - furo 56, 736, 743, 749 - nehringi 585 - gale 644, 654 - nigripes **641**, 761, 769, 770, 774 — galinthias 657 — nikolskii 644, 655 - glogeri 719, 731 — nippon 663, 676 - gulo 614, 618 - nivalis 51, 636, 637, 640, 641, 642, **643**, --- gulpsa 677 643, 644, 645, 647, 649, 650, 651, 652, - heptapotamica 771 652, 653, 653, **654**, 655, 655, **656**, 656, - heptneri 644, 654, 659 657, 662, 719 - herminea 663 — nobilis 771 - hibernica 676 — novikovi 719, 730, 713 — hodgsoni 712 - nudipes 641, 690 hungarica 719, 731, 754, 771 — numidica 657, 671 - iberica 657 occidentalis 771 - initis 677 — ognevi 664, 674, 737, 749 — intermedia 585, 587 - olympica 677

— orientalis 663, **675**, 737, **749**

749 Mustela pallida 656, 771 — peregusna 781, 783 wyborgensis 718, 729 - polaris 676 — vesoidsuno 644 — princeps 507, 531 - zibellina 56, 502, 507, 508 - punctata 644, 653 Mustelidae 54, 55, 57, 58, 491, 496, 497. — putorius 56, 501, 636, 641, 642, 719, 500, 785, 853, 911, 924 Mustelinae 497, 498, 502, 637, 641, 801, 721, 724, **736**, 737, 738, 740, 743, 744, 748, 749, 749, 754, 760, 761, 929 803, 817 - pygmaea 51, 644, 652, 653, 656 Mutica 10 - quelpartis 712 Mydaus 817 — raddei 691, 696 Mylarctos 404 - richardsonii 676 Myopus schisticolor 521 - ricinae 676 Myrmarctos 404 996 — rixosa 641, 644, 650, 657 — eversmanni 404, 408 - robusta 754 Mystacoceti 9 rothschildi 737, 749 - rupestris 507 N - russeliana 657 — sacana 695, 698 nair cf. Lutra - salva 677 namijei cf. Mustela - sarmatica 781, 783 Nandinia 49 - schnitnikovi 664, 676 Nasua 908, 911 - seclusa 677 Nasuella 911 - semplei 676 Nectogale 497 - sho 712 negans cf. Vormela - sibirica 637, 641, 643, 675, 690, **700**, Nepus 25 700, 701, 701, 703, 706, 706, 709, 710, - stelleri 25 710, 711, 711, 712, 724, 754, 837 niger cf. Canis - sibiricus 772 nigricans cf. Vulpes - stabilis 676 nivalis cf. Mustela - stantschinskii 749 Nyctereutes 60, 67, 63, 66, 67, 68, 68, 69, — stolizkana 644, 657 911 - streatori 677 — amurensis 69, 75 — strigidrosa 638, 641 — kalininensis 69, 75 - subpalmata 657 — koreensis 75 --- sylvatica 553 — orestes 75 - sylvestris 553 — procyonoides 59, 63, 64, **69**, 69, 70, 71, - talassica 772 74, 75, 75 - tatarica 924 - ussuriensis 75 — teberdina 664, 673 - viverrinus 66, 75 temon 686, 697 - tiarata 774 - tobolica 674 - tonkinensis 657 obscura cf. Vormela — transbaicalica 663, 675 — transsylvanica 719, 731 Odontoceti 9 - trettaui 644, 655 ognevi cf. Martes, Mustela, Putorius — turovi 730 orientalis cf. Canis, Mustela - tuvinicus 772 ornata cf. Vormela — varina 719, 731 Otariidae 53 -- vison 56, 641, 643, 723, 724, 924, 925, Otocyon 50, 58, 60, 62, 63 *928*, *928*, *930*, *931*, *932* — megalotis 63

Otocyoninae 62

vulgaris 636, 637, 644, 650, 655, 656,

Oxyaenidae 54 procyonoides cf. Nyctereutes Oxygous 96 Prorastomidae 23 Protosirenidae 23 Proteles 51 P Prototheria 10 Protungulata 10 Paenungulata 10, 15, 23, 24 pruinosus cf. Ursus Paleomeles 817 Pteronura 853, 854, 883 pallidior cf. Vormela - brasiliensis 494, 853 pallidus cf. Fennecus Pusa 882 pallipes cf. Canis - orientalis 884 pambasileus cf. Canis pusilla cf. Vulpes pamirensis cf. Ursus Putorius 636, 640, 641, 705, 723, 724, 736, Paralutra 854 742, 783, 929 Parameles 817 - alpinus 686 Paraonyx 498, 853, 854, 883 - amurensis 754 — congica 853 - arcticus 663 - microdon 854 - astutus 686 - philippsi 854 - aureus 754, 761, 772 Parataxidea 817, 818 - caucasicus 644 Paraxonia 10 — daurious 754 peregusna cf. Vormela - dinniki 644 Perissodactyla 10, 11, 54 - erminea 663 peninsularis cf. Martes eversmanni 753, 754 philippsi cf. Paraonyx - ferghanae 663 Pholidota 10 - foetidus 736 Pinnipedia 10, 11, 53, 54 - fontanieri 700 Pteronura 498 - furo 743 piriformis cf. Putorius - heptapotamicus 754 piscator cf. Ursus - kamtschatica 663 planicola cf. Vulpes — kaneji 663 Plesiogale 640 - kanei 663 Plesiogulo 616 — larvatus 753, 770 - brachygnatus 616 - michnoi 753 - monspessulanum 616 — nivalis 644 Plesiomeles 817 - nobilis 754 Poecilictis 498, 783, 785 - occidentalis 754 - libica 783 - ognevi 737 Poecilogale 498, 783, 785 - orientalis 737 Polyprotodontia 9 — pallidus 644, 754 Potamotherium 854, 883 — piriformis 737 Potos 907, 908, 911 — putorius 736, 737, 739, **754**, 761, 767, Prosimiae 9 772 Primates 10 - pygmaeus 644 Proboscidea 10, 23, 24, 54 - satunini 754 Procynodictis 60 — sibirica 663 Procyon 69, 908, 910, 911, 912, 912 - sibiricus 754 - cancrivorus 912, 914, 919 - stantschinskii 736, 739, 767 997 — lotor **56**, 912, **913**, 913, 915, 916, 917, - talassicus 754 - tuvinicus 754 Procyonidae 54, 55, 57, 60, 69, 402, 497, - verus 736 907, 909, 911 - vulgaris 736 Procyoninae 911, 912

putorius cf. Mustela

pygmaea cf. Mustela

R

rixosa cf. Mustela Rodentia 10, 11 Rohrwolf 140 rothschildi cf. Mustela rufus cf. Canis rüppeli cf. Fennecus Rytina 25 Rytina borealis 25 — cetacea 25 Rytiodinae 23

S

Sacalius 96 - aureus 96 sacana cf. Mustela Schaeffia 99 seistanica cf. Lutra Selenarctos 403, 404, 406, 414, 478 - ussuricus 478 severzovi cf. Meles Speothos 62 - venaticus 63 sibirica cf. Mustela sibiricus cf. Gulo, Meles, Ursus signata cf. Mellivora Simenia 62, 68, 99 — simensis 62 Simiae 9 Simocyoniae 62, 63, 383 Sirenia 10, 11, 15, 21, 22, 54 seistanica cf. Lutra Sivaonyx 854 Smilodon 50 Speothoninae 62 Speothos 58, 60, 62 — venaticus 59, 63 Spilogale 493, 498 spitzbergenensis cf. Alopex Stellerus 25 - borealis 25 Stenoplesictinae 497 Stromeriella 817 Subungulata 22 syriaca cf. Vormela syriacus cf. Ursus szetchuensis cf. Martes

Т

talassica cf. Mustela Tamias sibiricus 521 tatarica cf. Mustela Taxidea 493, 494, 498, 817, 818, 819 Taxodon 817 Taxus 816 Tayra barbara 616 teberdina cf. Mustela temon cf. Mustela Thalarctos 403, 404, 406, 455 - polaris 404 Thalassarctos 404 - ienaensis 455 — spitzbergenis 455 Thalassiarchus 404 Thos 96, 99 - vulgaris 96 thous cf. Lycalopex tianschanensis cf. Meles tiarata cf. Mustela tuvinicus cf. Mustela tobolica cf. Mustela Tomarctos 268 Theria 10 998 Tarsioidea 9 transsylvanica cf. Mustela Tremarctos 399, 403, 404, 406 - ornatus 401, 403, 406 trettaui cf. Mustela Trichechidae 15, 17, 23, 24 Trichechiformes 23, 25 Trichechus 15, 17, 18, 23, 24 - borealis 25

— borealis 25
— inuguis 16, 20, 24
— manatus 20, 24, 25
— senegalensis 20, 24
tschiliensis cf. Canis
Tubulidentata 10, 54
turcmenicus cf. Vulpes
tundrarum cf. Canis
turovi cf. Mustela

U

ungava cf. Alopex Unguiculata 10 ungavensis cf. Ursus Ursarctos 404 Urocyon 59, 62

- marinus 455, 460, 467, 468

456, 458, 461, 465, 467, 468

- maritimus 404, 406, 407, 411, 455, 455,

Urocyon cinereo-argentatus 63 - meles 816, 819 Ursavus 402 - melli 485 Ursi campestres 419 — meridionalis 407, 431, 431, 432, 433. Ursidae 54, 55, 56, 57, 60, 397, 401, 402, 434, 459 — minor 407 Ursus 398, 401, 403, 404, 404, 406, 407 — middendorffii 428, 436 - albus 618 - mupinensis 485 - americanus 399, 400, 404, 405, 406 - myrmecophagus 407 - arctos 399, 404, 406, 407, 407, 408, 411, - niger 407 *412*, *415*, *422*, 424, 428, **429**, 430, **431**. — normalis 407, 408 431, 432, 433, 433, 434, 435, 436, 436, - ornatus 404 437, 439, 451, 453, 459 - pamirensis 408, 434, 434 — aureus 407 - persicus 408 — baicalensis 408, 429 - piscator 407, 435, 436, 437, 459 beringiana 407, 436 — pruinosus 404, 407, **434**, 435, 437 - beringianus 435, 436 — polaris 455, 467 - brunneus 407, 436 — rossicus 408 - cadaverinus 407 — scandinavicus 408 — caucasicus 408, 431 - sibiricus 408 - cavifrons 436 - smirnovi 408, 431 — collaris 407, 429, 431 — spitzbergenensis 467 - crowtheri 428, 437 — stenorostis 408 - dinniki 431 - syriacus 407, 431, 432, 433, 434, 435, - eogroenlandicus 467 459 - formicarius 407 - thibetanus 404, 411, 478, 479, 481, 483, - formosanus 485 484, 485, 485 - gedrosianus 485 Ursus tibetanus 399, 403, 404, 406, 407, - grandis 408 414, 437 - griseus 407 — torquatus 478 - groenlandicus 469 - tyrannus 460 — gulo 615, 618 - ungavensis 469 - gyas 428, 436 - ussuricus 485 - hypernefes 408 — yeniseensis 408, 429, 432, 433, 436, - indicus 804 437, 459 - isabellinus 407, 434, 435, 439, 453 yessoensis 404, 408 - japonicus 485 ussuricus cf. Ursus — jenaensis 467 ussuriensis cf. Nyctereutes - jessoensis 406 — kamtschatica 407 - kolymensis 408, 429 - labradorensis 469 vancouverensis cf. Gulo - lagomyarius 408 Vetularctos 406 - laniger 485 Vishnuonyx 854 - lasiotus 404, 408, 436, 436 Viverra aterrima 884 - lasistanicus 408, 433 — capensis 801, 804 - leuconyx 408, 434 — lutreola 636, 718 — longirostris 407 ratel 801 — lotor 912, 913 Viverridae 54, 55, 497 — luscus 618 viverrinus cf. Nyctereutes - mandchuricus 408 Vormela 498, 501, 501, 781, 781, 782, 783

- alpherakyi 794

- chinensis 798

Vormela euxina 784, 794 — flavescens 66, 319, 333, 334, 337, **340**, - intermedia 794 340, 360 koshevnikovi 783, 794, 795, 796, 797 - fulva 327, 341 - negans 784, 796, 797 - griffithi 341 - harrimani 341 — obscura 784, 794 — ornata 784 - hoole 341 - pallidior 784, 795, 796 -- huli 320 - peregusna 782, 783, 783, 784, 784, 785, — induta 341 788, 790, 793, **794**, 795, **796**, 797, 798 — ischnusae 341 - sarmatica 784, 794 -- jacutensis 320, 339 - syriaca 784, 797 — japonica 341 999 - tedschenica 783, 794 — kalmykorum 273, 280 Vulgaris cf. Mustela - kamtschadensis 319, 339 Vulpes 62, 63, 68, 69, 99, 194, 196, 265, — kamtschatica 319, 339 265, 268, 277 - karagan 320 - kenaiensis 341 - abjetorum 341 — aegyptiaca 341 kiyomassai 320, 339 — alascenis 341 — krymea-montana 319 — krymensis 338 - alopex 319 alpherakyi 319, 338, 338 - kurdistanica 319, 338 — alticola 320, 338 - lagopus 196 anadyrensis 319, 339 — bengalensis 63 - anatolica 341 - leucopus 319 - arabica 341 — macroura 341 — atlantica 341 - melanotus 339 — bangsi 341 - montana 341 - barbara 341 — monticola 341 - bengalensis 268, 272, 327 — necator 341 — beringiana 339, 339, 341 - nigra 273, 281 - beringianus 196 - nigricans 269 - cana 63, 66, 266, 268, **269**, 269, 269, ochroxantha 320, 340 270, 271, 272, 327 - palestinae 341 caragan 336, 339, 340 — pamirensis 320, 340 - cascadensis 341 — peculiosa 341 — caucasica 319, 338 — planicola 341 -- chama 268 — pusilla 341 cinerascens 319, 340 - pusillus 319 — communis 265 - regalis 341 — coloregriseo 319 - rubricosa 341 - corsac 63, 66, 266, 268, 273, 274, 275, - rüppeli 268 *276*, *279*, **280**, **281**, 315, 327 -- schrenkii 320, 339, 341 - crucigera 319, 320, 337, 341 scorodumovi 273, 281 - crymea-montana 338 - septentrionalis 319, 336 - crymensis 319 — sibirica 339 - daurica 320, 339, 339 - sibiricus 319 — deletrix 341 - silacea 341 — diluta 320, 337, 337, 339, 340 - splendens 319, 340, 340 dolichocrania 320, 325, 336, 339 - splendidissima 320, 339, 341 — eckloni 281 - stepensis 319, **337**, 338 - ferganensis 320, 333, 340 - tarimensis 319 --- ferrilata 268, 272, 327 - tobolica 320, 339, 340

- tschiliensis 319

- ferrilatus 63, 281

Vulpes turcmenica 273, 280, 315

— ussuriensis 319, 339

- velox 63

- vulgaris 319

vulpes 56, 58, 63, 64, 66, 66, 266, 268, 318, 319, 320, 321, 326, 327, 329, 330, 333, 334, 336, 336, 337, 337, 337, 338, 339, 339, 340, 340, 341, 360

Vulpicanis 96

W

wilsoni cf. Mellivora

Y

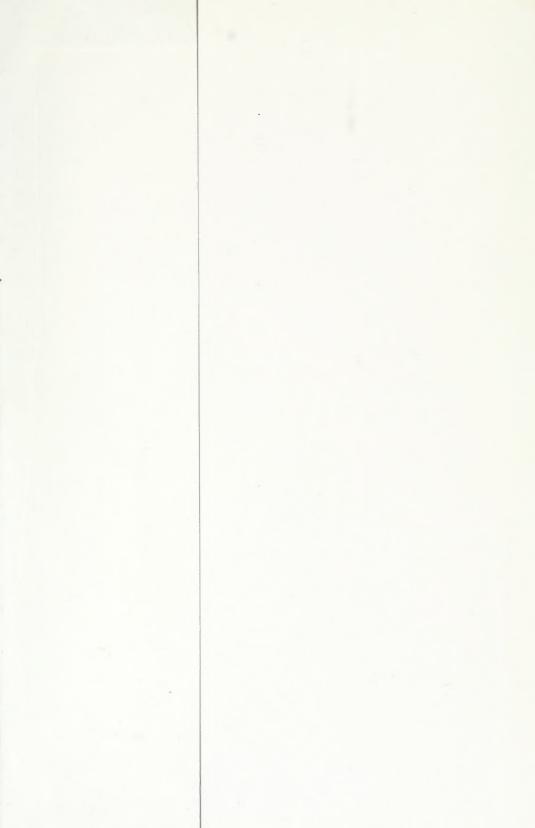
yeniseensis cf. Martes, Ursus yuenschanensis cf. Martes

 \mathbf{Z}

zerdus cf. Fennecus zibellina cf. Martes Zibellina 502 Zorilla libyca 783







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The order of pinnipeds or seals (Pinnipedia) is described in this volume. The cohort of ungulates and carnivores represented in soviet fauna by orders of artiodactyls, and perissodactyls, sirenians, carnivores, and pinnipeds thus came to an end and the cohort of whales (Mutica) commences. The toothed whales are described in this volume.

While it has not always been possible to maintain a totally uniform description of the genera and species as in the volumes already published, in spite of every effort to do so, the sequence has been adhered to, with some exceptions, in the case of Pinnipedia. But, it was impossible to use same format in describing the toothed whales (Odontoceti). Only a brief morphological description has been given for many species, which is more or less adequate for identifying the species. General information on their distribution and fragmentary biological data are also given. In some cases the total absence of such information is indicated.